LAMPYRIDAE OF AUSTRALIA (COLEOPTERA: LAMPYRIDAE: LUCIOLINAE: LUCIOLINI)

L.A. BALLANTYNE AND C. LAMBKIN

Ballantyne, L.A. & Lambkin, C. 2000 12 31: Lampyridae of Australia (Coleoptera: Lampyridae: Luciolinae: Luciolini). *Memoirs of the Queensland Museum* **46**(1): 15-93. Brisbane. ISSN 0079-8835.

The flashing firefly fauna of Australia (Lampyridae: Luciolinae: Luciolini) is revised recognising 25 species in 4 genera. All genera are keyed from males and redescribed. All species are keyed from males, and from associated females and larvae. Existing species are redescribed and 8 new species described. Newly associated females and larvae are described. Species distributions are recorded and mapped. *Luciola* subgenus *Luciola* includes 6 species: *australis* F., *cowleyi* Blackburn, *dejeani* Gemminger, *flavicollis* MacLeay, *nigra* Olivier (the last two have larvae described), and *orapallida* sp. nov. which is described from males, females and larvae. *L. dejeani* may not be Australian and its status is discussed. *L. scutellaris* Lea and *L. humilis* Olivier now stand under *Luciola nigra* Olivier. The type specimen of *L. australis* is reconsidered. *Atyphella* Olliff comprises 23 species including 7 new: *atra* Lea, *brevis* Lea, *conspicua* sp. nov., *ellioti* sp. nov., *flammans* Olliff, *flammulans* sp. nov., *immaculata* sp. nov., *inconspicua* (Lea), *lewisi* sp. nov., *lychnus* Olliff, *majuscula* (Lea), *monteithi* sp. nov., *olivieri* Lea, *scintillans* Olliff, *similis* sp. nov.; *costata* (Lea) is transferred to *Atyphella* from *Luciola*. Females are described for *atra*, *costata*, *flammans*, *inconspicua* and *olivieri*, and larvae for *atra*, *flammans*, *majuscula*, *olivieri* and *scintillans*. The following non-Australian species are assigned to *Atyphella*: *aphrogeneia* (Ballantyne), *carolinae* Olivier, *huonensis* (Ballantyne), *leucura* Olivier, *marginipennis* (Guérin), *obsoleta* Olivier, *wolfi* (Olivier). *Pteroptyx* Olivier is represented by *P. cribellata* Olivier and *P. platygaster* (Lea), raised from synonymy with *P. cribellata*. *Pyrophanes* Olivier in Australia is based on *P. beccarii* Olivier, under which *Luciola complicata* Lea is synonymised. Lectotypes are designated for *Atyphella brevis*, *A. flammans*, *A. inconspicua*, *A. lychnus*, *A. majuscula*, *A. olivieri*, *A. scintillans* and *Pteroptyx platygaster*. The first phylogenetic analysis undertaken on the Luciolinae reveals preliminary directions for its taxonomy. The status of the genus *Atyphella* Olliff is supported and is expanded here. A *Luciola*/*Pteroptyx* clade includes species of 6 genera (*Pteroptyx*, *Pyrophanes*, *Colophotia*, *Lampyroidea*, *Bourgeoisia*, and 2 subgenera of *Luciola*) and needs to be addressed from a wider perspective before definitive changes are made. Nine Australian species identified in this clade are assigned to existing genera. Initial cladistic analyses could not be completed because of a computer program limitation on the number of most parsimonious trees that could be saved. Several methods to overcome the problem of large numbers of most parsimonious trees, generated because of the high proportion of missing larval and female data in the matrix, are investigated. The significance of female aptery, morphological adaptations of the male and their behavioural significance, the nature of the labrum, distribution and possible origins of the Australian fauna are also discussed. ☐ *Insecta, Coleoptera, Lampyridae, Luciolini, Australia, taxonomy, behaviour, morphology, phylogeny, missing data.*

Lesley Ann Ballantyne (email: lballantyne@csu.edu.au), Charles Sturt University, School of Agriculture, PO Box 588, Wagga Wagga 2678, Australia; Christine Lambkin, Department of Zoology and Entomology, University of Queensland, St Lucia 4072, Australia; *received 22 October 1999.*

The Australian Lampyridae are all flashing fireflies (i.e. males and females have light organs, which are used to attract the sexes for mating). They occur mainly along the eastern seaboard of Australia from Cape York Peninsula to the Illawarra region in New South Wales (Moore. 1989) in a discontinuous pattern paralleling for the most part rainforest or mangrove regions. This distribution and the paucity of species relative to New Guinea reflect the discontinuous rainforest pattern. A few species occur across northern coastal Australia (Northern Territory and Gulf of Carpentaria) but nothing is known of their ecology. Fireflies are restricted by a combination of temperature and humidity, partly because of their soft exoskeleton, but also because these conditions affect the distribution of their food source, which is mainly small land snails and slugs.

Twenty-five species and 4 genera are treated here. A single female from Murray I. in Torres Strait is an outlier representative of a basically New Guinea species and it is more appropriate for its formal taxonomy to be dealt with in the broader treatment of the whole New Guinea fauna (Ballantyne, in prep.). It is included here in the key to females of *Luciola* only, as *Luciola* species A.

The Australian fauna is exclusively Luciolinae, a subfamily distributed around the warmer parts of the world except for South America, and distinguished by the possession of only 6 visible abdominal sternites in the male and the loss of abdominal sternite 8. There is no similar loss in the female. Ballantyne (1987a,b) discussed abdominal segmentation in Luciolinae; the 6 visible abdominal sternites belong to actual segments 2-7, with the light organs in the male on sternites 6 and 7, and in the female on sternite 6 only. Since abdominal sternite 8 is lost in the adult male, the visible terminal segments are thus sternite 7 and tergite 8. Remnants of sternite 1 may occur at the base of the abdomen as small, lateral, slightly sclerotised plates in an otherwise membranous area (Ballantyne, 1992).

This study defines species by morphological features, using all life cycle stages when available. Little information is available on the light patterns, shown by McDermott (1910) and Lloyd (1966) to be important in enabling accurate species differentiation. A few studies in the Australasian and Indomalaysian areas have thus far characterised fireflies by behavioural (viz. flashing data) as well as by more conventional means (Ballantyne & McLean, 1970; Lloyd, 1972, 1973b; Ballantyne & Buck, 1979; Ballantyne, 1987a). However those studies indicate the usefulness of an initial taxonomic study to guide behavioural work (e.g. Ballantyne & McLean, 1970) and of a morphological re-evaluation once light patterns are known (e.g. Ballantyne, 1987a). Since a similar approach is expected here label data is quoted in full to allow accurate relocation of all specimens examined, and any consistent variability in features such as colouration is noted with the specimen listing.

Calder (1998) catalogued the Australian Lampyridae following Ballantyne (1992) and presented an historical overview.

None of the Australian genera treated here is endemic and two, *Pteroptyx* and *Pyrophanes*, are represented in Australia by very few species. Cladistic analysis of relationships based on only Australian species would be limited; instead, a wider interpretation is attempted using 43 lucioline taxa. While this analysis supports the retention and extension of the genus *Atyphella*, relationships of the other three genera remain problematical. The Australian species are therefore assigned to four existing genera and subgenera, and redescribed from their Australian representatives only. However we anticipate that as certain groups are more thoroughly investigated other genera and subgenera will be defined.

Ballantyne provided the taxonomic descriptions and all figures and is to be regarded as the sole author of the new species. Lambkin undertook the cladistic analysis and wrote the section on phylogeny based on information provided by Ballantyne.

MATERIAL AND METHODS

This study examined over 3,000 specimens including over 200 holotypes, lectotypes and paratypes. Most original specimens studied are in the Queensland Museum. Specimens in Australian collections were identified during 1997-1999.

Types if located were re-examined. Their identity was not always clear from the labels and LB followed Calder (1998) and the original descriptions in determining their status. Some confusion is overcome by lectotype designation.

Most adult specimens examined during this study have been pinned. Some live specimens were killed, fixed and preserved in 70% ethanol. Such treatment made manipulation and dissection easier, but colour patterns may be obscured by the increased transparency of the elytra and pronotum; some shape distortion occurred; the extent of some light organ material became unclear, especially if the specimen was pinned after being in alcohol.

Larvae were killed, fixed and preserved in 70% ethanol. Many larvae examined were collected over 30 years ago and some had been described (Powell, 1964); re-examination revealed some colour fading. Freshly collected and preserved larvae were described where possible.

The Dept. of Zoology and Entomology at the University of Queensland houses a large collection of alcohol preserved Lampyridae in tubes numbered with prefix 'T'.

An important component of the collections studied is the numerous fireflies collected in the Wet Tropics Zone of North Queensland by Queensland Museum personnel since 1980 under the leadership of Dr G.B. Monteith. This intensive survey attempted to systematically collect all the rainforested mountain systems of this complex, high-rainfall, subcoastal region between Cooktown and Townsville. Monteith (1995) divided the Wet Tropics into 19 mountain blocks, each separated by natural barriers and/or dry corridors. These were used by Baehr (1995) in his analysis of the carabid genus *Philipis* and are employed herein (Figs 9, 10, 11 and 13).

SPECIMEN LISTS. These are given in a standard format as follows. The first entry for TYPE gives full label data for primary type/s, with deposition, registration number, whether examined and lectotype procedures. For new species all additional specimens are made paratypes. Under the heading MATERIAL all specimens are summarised. An initial statement gives total numbers. Specimens are listed by Australian state with Queensland divided into northern (N QLD: north of Bowen), central (C QLD: Gladstone to Bowen) and southern (S QLD: south of Gladstone) sectors. Localities are listed from north to south. Data is listed in sequence: latitude, longitude, locality name, date, collector/s, museum deposition. The locality is not repeated for separate collections from same locality, and museum deposition is only entered when it changes from last citation.

ABBREVIATIONS. *Collection Repositories*. LB is grateful to the following institutions from which collections were borrowed. They are listed with their abbreviation used and the curators with whom LB dealt: AM, Australian Museum, Sydney (M. Moulds); ANIC, Australian National Insect Collection, CSIRO Canberra (T. Weir); BPBM, Bernice P. Bishop Museum, Honolulu, USA (A. Samuelson); BMNH, Natural History Museum, London (J. Beard); CAS, Californian Academy of Sciences, San Francisco; DPI, Dept. of Primary Industry, Mareeba, Queensland (R. Storey); UQ, Dept. of Zoology and Entomology, University of Queensland (M. Schneider); MAGNT, Museum and Art Gallery of the Northern Territory (G. Brown); MM, Macleay Museum, University of Sydney (D.S. Horning); MCG, Civic Museum, Genoa, Italy (R. Poggi); MNHP, Musèum National d'Histoire Naturelle, Paris, France (J. Ménier); MV, Museum of Victoria, Melbourne (K. Walker); OTT, National Museum of Natural Sciences, Ottawa (F. Génier); QM, Queensland Museum, Brisbane (G. Monteith); SAM, South Australian Museum, Adelaide (E. Matthews).

Collectors. EB, Ev Britton; GB, George Brooks; CB, Chris Burwell; BC, Bryan Cantrell; IC, Ian Common; DC, Doug Cook; HH, Henry Hacker; HJ, Heather Janetzki; SH, Simon Hamlet; JL, John Lawrence; DKM, David McAlpine; GBM, Geoff Monteith; SRM, Sybil Monteith; LP, Lesley Powell (married name Ballantyne); RS, Ross Storey; GT, Geoff Thompson; MU, Murray Upton; JLW, Lea Wassell; TW, Tom Weir; DY, David Yeates; AWH, A.Walford-Huggins; PZ, Paul Zborowski.

Descriptions. ASD, distance between antennal sockets; ASW, greatest diameter antennal socket; EO, ejaculatory orifice aedeagus; FS, antennal flagellar segments; GHW, greatest head width, across eyes, measured parallel to ASD; LL, lateral lobe aedeagus; MFC, metafemoral comb; ML, median lobe aedeagus; MPP, median posterior projection sternite 7; MS, mesoscutellum; SIW, smallest interocular width (measured parallel to ASD, ASW).

Other Abbreviations. FIT, flight intercept trap; NP, National Park; PF, pitfall; RF, rainforest; SF, State Forest.

Latitude and longitude are abbreviated e.g. 17.15S = 17 degrees 15 minutes south.

MEASUREMENTS. Dimensions (in mm) should not be taken as absolute as most Lampyridae are soft bodied and subject to distortion. Measurements are further affected by the condition and age of the specimen, whether wet or dry preserved, and any delay between capture and killing. Except for total length, most dimensions are used comparatively as indicated below.

Length of pronotum is median length; width of pronotum is measured at the widest region. The length of winged specimens is sum of median lengths of the elytron and pronotum. As the pronotum tends to droop in pinned specimens their total length will usually appear to be slightly shorter than the figure given. The head is not included in overall body length because it may or may not protrude in front of the pronotum. Brachelytral female length is median length of the pronotum plus an estimation of the non-extended length of the rest of the body (most of the brachelytral females measured are quite gravid). For larvae the dimensions of the protergum and the relative length of abdominal and thoracic terga is less subject to variation than absolute length.

Adult head measurements refer to the anterior aspect. Greatest head width (GHW) is taken horizontally across and including the eyes at the widest point. Smallest interocular width (SIW) is taken between the eye edges, just above the antennal sockets. The smallest distance separating the antennal sockets (ASD) compared to the width of a socket (ASW) is more useful than the absolute measurement of either.

Larval head length is median length of the frontoclypeus; width is maximum dorsal width (not including the simple eyes if they protrude beyond the lateral head margins).

DISCUSSION OF CHARACTERS. Characters and dissection methods follow Ballantyne & McLean (1970) and Ballantyne (1987a). For convenience some are repeated. The taxonomy is male-based as difficulties exist in associating the sexes unless taken *in copula*. Female characters are described only when they differ from those of the male. Wherever possible features are described comparatively (e.g. elevation of elytral interstitial lines is related to sutural ridge elevation; proximity of the antennal sockets is a function of their diameter).

Pronotal width is characterised: width across posterior third either subequal to (Fig. 19C-E), narrower than (Fig. 19A) or wider than (Fig. 1A-D,F,G,I-L, Fig. 19B) width across anterior third. Lateral pronotal margins are: subparallel (Fig. 19C), divergent along at least anterior half (Fig. 1A-D,F,G,I-L), divergent along their length, or pronotum is widest across the middle and lateral margins converge anteriorly and posteriorly (Fig. 1E, H). Anterolateral corners are rounded, often obtusely (e.g. Fig. 1A-D), or pointed (Ballantyne, 1968: fig. 130). Posterolateral corners are rounded (Fig. 1A-L), or approximately right-angled (Fig. 19C,E). An explanate lateral margin may be wider in the posterior half, or not.

A maximum of 4 elytral interstitial lines is numbered 1 (nearest suture) to 4 (nearest lateral margin). Well defined interstitial lines are elevated and thickened at least as much as the sutural ridge; evanescent lines are scarcely if at all elevated, often obliterated anteriorly and posteriorly. Degree of development of interstitial lines is further compared one to the other on the same elytron.

The shape of the deflexed elytral apex uses comparisons of lengths across the posterior margin of the deflexed apex, the outer (epipleural) margin, and the inner (sutural) margin (see Fig. 20K). The elytral epipleuron and a distinct sutural ridge may extend along all or part of the margin to the apex.

The relative size, depth and approximation of punctures on the pronotum and the elytra can be ascertained under high power of the stereo dissecting microscope (× 40).

McDermott (1964) distinguished the Photurinae with a 'membranous labrum arising from the ventral surface of a strongly sclerotized clypeus'. The nature of the labrum was reinterpreted by John Lawrence (ANIC): in the cantharoids there is probably never a well developed clypeus separated from the frons by a complete frontoclypeal suture. In most Lampyridae the labrum is at least slightly sclerotised and separated from the clypeus by a strip of membrane. In most Luciolinae the labrum is free. The anterior strongly sclerotised plate on the Photurinae head is here interpreted as the labrum.

Proximity of eyes above the labrum (SIW/GHW) is measured as close (1/6–1/15), moderately (> 1/6 but < 1/2), or widely separated (1/2 -1/3). Separation of eyes on the ventral head surface is measured just behind mouthpart complex relative to the GHW measured at the same point. In *Atyphella*, a junction between the frons and the vertex may be conspicuous and acutely margined or rounded (Fig. 2C,F,G,I), or not clearly evident (Fig. 2A,D,H). Frons height is measured from the top of the antennal sockets to the middle of the frons/vertex junction relative to the antennal socket width (ASW). Depression of the vertex is minimal (barely excavated if at all), or moderate to deep. A posterior excavation of the eye if present is visible from the side (Ballantyne, 1968: figs 144, 147-150).

In the Luciolinae the head may be concealed from above by retraction into the cavity beneath the pronotum; lateral margins even if explanate do not contribute to this concealment. In *Photuris* spp. (considered here as an outgroup) the head is too large to be retracted into the pronotal cavity and the explanate anterior and lateral margins contribute to head concealment. The Luciolinae head is either greatly exposed (the head cannot be retracted into the pronotum), slightly (some of the posterior head is retracted beneath the pronotum) or completely concealed (not visible from above). Mouthparts are small and probably non-functional when antennal sockets are contiguous and mandibles and palpi are reduced.

Ballantyne (1987a: 119) characterised abdominal features including the ventral face of tergite 8 and light organ area, which are used here. Tergite 8 may bear ventrally a 'longitudinal trough' housing the aedeagal sheath, and margined laterally by elevated longitudinal 'ridges'; the area lateral to the ridges may be flat (Fig. 20C) or depressed ('lateral troughs') (Fig. 26C,D). Ballantyne (1987a: 119) defined 'flanges' as 'variable shaped paired projections (that) arise from the anteromedial area of the lateral margins (of the downturned lateral margins on the ventral face of tergite 8)'; these partially enfold the aedeagal sheath in its resting position. Flanges are redefined here as: distinctly prolonged structures at the anteromedial area of the downturned lateral margins of tergite 8, separated from the rest of the downturned lateral margin by some narrowing at their bases; apically rounded or pointed, broad or narrow, sometimes asymmetrical. As redefined *Luciola australis* F. (Ballantyne, 1988) does not possess flanges.

A median longitudinal carina and/or 'trough' may occur between light organ halves in sternite 7 (Ballantyne & McLean, 1970: fig. 3D,G,F) and a depression ('dimple') anterior to the MPP (Fig. 20K). Developments along sternite 7 posterior margin are: a median posterior projection (MPP) may be developed (Fig. 3A-D, F, J; Fig. 4C, H; Fig. 20A,D,G,J; Fig. 26A); LPP are posterior projections of the postero-lateral corners of sternite 7 (Fig. 20J,M; Fig. 26A,B); incurving lobes and pointed projections may occur (Fig. 26A).

Female head form variability correlates with the extent of elytra (and consequently flight ability) and is referred to Figure 6. Winged females' heads are similar to those of the males except for smaller eyes and a slighter depression of the vertex; the head may be exposed or concealed beneath the pronotum, and mouthparts are always well-developed (Fig. 6B). Brachelytral females have very small concealed heads, small widely separated eyes, widely separated antennal sockets, a shallowly depressed vertex, and the anterior portion of the head capsule in front of the eyes and including the antennae, is prolonged anteriorly (Fig. 6D,E). Mouthparts may be functional or not.

Reliable sex associations are made by taking specimens *in copulo*. Tentative assignments of females may be made on the basis of label data only; these are so indicated in the descriptions. It is reasonable to assume conspecificity where males of only one species are flying and females are observed flashing in apparent response to them. When such associations are made it is so indicated in the descriptions. Larval associations are confirmed by rearing unless indicated otherwise.

All descriptions are ordered in that the entire dorsal surface is examined first and then the ventral, facilitating examination of specimens. Specimens thus do not have to be repeatedly turned.

GENITALIA PREPARATION. The method of extraction of the aedeagus described in Ballantyne & McLean (1970: 229-230) was modified to preserve the integrity of the aedeagal sheath and to allow observation of the ventral face of tergite 8. The abdomen of pinned specimens was removed and softened. Terminal tergites and sternites were separated along the membranous lateral line and the tergites folded back to allow examination of the nature of the ventral face of tergite 8 and the dorsal face of the aedeagal sheath, which could then be left in place. Longitudinal muscles arising on the anterior prolongation of the aedeagal sheath sternite (Ballantyne, 1987b: fig. 2H) and which insert in the base of the aedeagus were then severed. The aedeagus was extracted by pulling it carefully in an anterior direction, grasped by fine forceps. Dried specimens were rehydrated and the aedeagus pulled from the body making it visible but still attached; this did not however allow observation of the nature of the aedeagal sheath.

MORPHOLOGY OF LAMPYRIDAE

This morphological discussion is based on Australian representatives.

Soft bodied, somewhat flattened insects. Adults with pale luminescent organs beneath the 5th visible, or actual 6th abdominal sternite in the female, and beneath the 5th and 6th visible, or actual 6th and 7th abdominal sternites, in the male. Pronotum pale coloured, usually orange, or cream, often with median dark markings; elytra often semitransparent if pale; sometimes pale yellow or orange with terminal dark markings; otherwise pale or dark brown, sometimes with paler orange or yellow basal, and/or lateral and/or sutural margins; interstitial lines often paler than rest of elytron.

MALE. Pronotum often with lateral margins explanate and flattened; in *Atyphella* wider than long (W/L 1.5-2.6) with anterolateral corners usually rounded and lateral margins often diverging posteriorly (Figs 1, 2); in *Luciola*, *Pteroptyx* and *Pyrophanes* not much longer than wide (W/L

1.2-2.0), lateral margins not diverging posteriorly and approximately subparallel (Fig. 19 A,C-E). Legs with flattened tibiae lacking apical spurs; tarsi 5 segmented, with 4th tarsomere bilobed and 5th elongate, slender and entire; tarsi with 2 basally toothed entire claws at apex; hind tibiae curved and hind femora swollen and curved in *Pyrophanes*, not so in *Atyphella*, *Luciola* and *Pteroptyx*. MFC present in *Pyrophanes* (Fig. 26H); absent in *Luciola*, *Atyphella* and Australian *Pteroptyx* (Ballantyne, 1987a). Elytra with short, often dense pubescence; elytral epipleura broad at base; elytra covering abdomen completely at rest; a maximum of 4 interstitial lines barely discernible or variously developed; apex deflexed in *Pteroptyx*; hind wings fully developed and all males presumed capable of flight. When viewed from above the head may be completely covered, or at least part of head is covered by pronotum in withdrawn condition in many *Atyphella* (Figs 1, 2), or head may be incapable of being covered by pronotum in withdrawn condition in *Luciola*, *Pteroptyx* and *Pyrophanes*, where less than 1/3 of head is covered; the comment 'head is concealed by explanate pronotum' (Lawrence & Britton, 1991: 640) does not refer to Australian species where the head cannot be concealed in many species, or only the lateral pronotal margins are explanate and do not contribute to concealing the head from above; eyes very large, often closely approaching ventrally in *Atyphella* and almost contiguous ventrally in *Luciola cowleyi*; ocelli absent; antennae filiform, 11 segmented (less than 11 segmented in some *A. scintillans* and *A. ellioti*) and inserted at front of head just above the labrum; antennal length 1-2 × GHW; antennal sockets close, often contiguous, never separated by more than twice ASW; labrum separated from clypeus by suture, labrum small and about as wide as long in *Atyphella* (Fig. 2), and about twice as wide as long in *Luciola*, *Pyrophanes* and *Pteroptyx*; clypeus indistinct, frons reduced, most of head area between eyes represented by the vertex, which is often deeply depressed; (head capsule interpreted from Stickney, 1923). Mouthparts very hairy and usually well developed although adults may not feed; mandibles curved, perforated by a canal, acutely pointed at apices, which cross at rest; mandibles with a well developed hairy prostheca at their inner basal angle; maxillae densely hairy, palpi 4 segmented with enlarged apical segment; all areas recognisable although galea and lacinia are imperfectly separated; labium with mentum and submentum small and weakly demarcated; palpi 3 segmented, apical segment much smaller than apical segment of maxillary palpi, and slender and elongate in most *Luciola*, *Pteroptyx*; laterally compressed with inner margin excised in some *Atyphella*. Abdomen with 6 visible sternites belonging to actual segments 2-7, and light organs beneath sternites 6 and 7; abdominal sternite 1 appears as paired lateral islands of cuticle in *Pteroptyx*, and is hidden by the hind coxae at rest (Fig. 20J; Ballantyne, 1987a); light organ entire in sternite 6 although retraction from lateral and posterior margins may be a post-mortem change; light organ entire in sternite 7 in *Luciola*, *Pteroptyx* and *Atyphella* (Figs 3, 4, 20), although often retracted into anterior half in *Luciola* and *Pteroptyx*; light organ bipartite in sternite 7 in *Pyrophanes* (Fig. 26). Posterior margin of sternite 7 variously developed and described in detail here and in Ballantyne (1987b). Aedeagal sheath (Fig. 21) lacking lateral protuberances (paraprocts) except in *Pyrophanes*. Aedeagus a simple elongate, often slender, structure comprising median and lateral lobes with no accessory processes and a simple membranous basal piece (Figs 5, 21).

FEMALE. Macropterous and presumed capable of flight (unless female is very gravid) in some *Atyphella*, and all known *Luciola*, *Pteroptyx* and *Pyrophanes*. Elytra and hind wings variously reduced in some *Atyphella*, females never completely wingless, and apices never deflexed. Head always covered by pronotum at rest, eyes smaller than those of males (Fig. 6). In *Luciola* and macropterous *Atyphella* females the eyes are little reduced, the GHW is always > twice SIW, and the mouthparts insert close to the anterior eye margin (Fig. 6B); in brachelytral *Atyphella* the eyes are much reduced, the GHW is about 2 × SIW, and the head is prolonged beyond the anterior eye margins (Fig. 6D,E). Mouthparts usually well developed. MFC absent and no legs with swollen or curved segments. Light organs entire beneath sternite 6 only, although sternite 7 may bear pale fat body patches. Abdomen with 7 visible sternites (segments 2-8), tapering posteriorly.

LARVA. Elongate, slender, tapering somewhat in front and behind; 3 thoracic and nine abdominal segments; terga more heavily sclerotised than venter; all body segments except the last with a median dorsal longitudinal groove (Figs 7, 12, 15); and laterally explanate in *Atyphella*, but not so in *Luciola*, coloured cream, yellow and/or brown. Head when retracted invisible beneath pronotum; with a single simple eye on each side. The meso- and metathoracic sterna comprise (Fig 7) an anterior 'complementary segment', bearing spiracles, and a posterior leg bearing area; (the complementary segment has no intrinsic segmental muscles or other segmental structures and is a fold of the sternal integument not extending to the terga — Martin (1916) attributed it to the segment in front); ventrolateral sutures delimit epipleural areas on all but the terminal segment. The meso and metathorax bear 2 epipleural areas per segment, the anterior plate bearing the spiracles. Each sternal area of abdominal segments 4-11 carries laterally narrow paired pigmented epipleural areas of which the most lateral bears the spiracles; complementary segments are absent; light organ present beneath abdominal segment 11 (i.e. penultimate) and the light is visible from above and below; abdomen terminated by a series of eversible filaments or pygopods (Domagala & Ghiradella, 1984).

Powell (1964) described larval morphology for certain *Luciola* species, Ballantyne & Buck (1979) the larva of *Luciola aphrogeneia*, (assigned here to *Atyphella*) and some aspects of larval morphology of *Luciola pudica* (= *L. australis*). Non-Australian *Pteroptyx* and *Pyrophanes* larvae lack laterally explanate tergal margins (Ballantyne & McLean, 1970; Ballantyne, 1987a,b; Blair, 1927).

BIOLOGY OF LAMPYRIDAE

Larvae and pupae faintly luminous; the larval light a continuous glow visible equally well from either surface; extinguished if the larva is disturbed; luminosity of eggs not observed. Sivinski (1981) suggested certain adaptive significances of the larval light. In adult males the light is emitted from special light organs on visible sternites 5 and 6, and in the female from the visible 5th sternite. Light is under nervous control and is emitted in a series of controlled flashes in both sexes; in North American and New Guinean species, there exists a complex dialogue in male flash pattern and duration, and female response, which serve as a means of attracting the sexes and maintaining species identity (review of light production in Lampyridae, Lloyd 1971, 1973b, 1977). Preliminary observations suggest the same is true of Australian fireflies. Australian species are restricted to moist areas (e.g. mangrove river flats, rainforest and relict rainforest) which will maintain a population of small land snails, on which the larvae have been observed to feed. In European species the larval prey is paralysed by injection of the secretion of a pair of acinose glands at the anterior end of the alimentary canal, through the tubular, sharply pointed mandibles. The larva imbibes the liquefied tissues of the prey. Larvae of *Luciola australis* appear to use their abdominal filaments to aid in forward progression; the terminal segment of the abdomen is brought forward under the more anterior segments (while the filaments are partly exserted) in the manner reminiscent of a looper caterpillar (Lepidoptera: Geometridae) (Powell, 1964).

ARRANGEMENT OF TAXA IN THE LUCIOLINAE

The Luciolinae is treated here in the form devised by McDermott (1966) (with subsequent additions in bold type).

LUCIOLINAE
LUCIOLINI

- ***Atyphella*** Olliff (restored to generic level by Ballantyne in Calder, 1998)
  - Type species *Atyphella lychnus* Olliff
- *Bourgeoisia* Olivier
  - Type species *Luciola antipoda* Bourgeois
- *Colophotia* Dejean
  - Type species *Lampyris praeusta* Eschsch.
- *Luciola* Laporte
- Subgenus *Luciola* s. Str.
  - Type species *Luciola pedemontana* Mots. 1853
- Subgenus *Hotaria* Yuasu 1937
  - Type species *Luciola parvula* Kiesenw. 1874
- Subgenus *Photuroluciola* Pic
  - Type species *Photuroluciola deplanata* Pic 1931
- Subgenus *Pygoluciola* Wittmer
  - Type species *Pygoluciola stylifer* Wittmer 1939
- **Subgenus *Pygatyphella*** Ballantyne 1968. Two species of this subgenus including the type species *obsoleta* Olivier are assigned to *Atyphella*. The remaining species are yet to be investigated.
- *Lampyroidea* Costa
  - Type species *Lampyroidea syriaca* Costa 1875
- *Pteroptyx* Olivier
  - Type species (see discussion)
- *Pyrophanes* Olivier
  - Type species *Pyrophanes similis* Olivier
- Curtosini
- *Curtos* Motschulsky
  - Type species *Curtos mongolicus* Motschulsky

KEY TO AUSTRALIAN GENERA USING ADULT MALES

1. Elytral apices deflexed (Fig. 20J,K) . . *Pteroptyx* Olivier
   Elytral apices not deflexed 2
2. Metafemoral comb present (Fig. 26H); light organ bipartite in sternite 7 (Fig. 26A); aedeagal sheath symmetrical, bearing paraprocts (as in Fig. 21B); lateral lobes of aedeagus about 4/5 length of median lobe and fused for most of their dorsal length and apices not visible ventrally (Fig. 26E-G) . . . *Pyrophanes* Olivier
   Metafemoral comb absent; light organ entire in sternite 7; aedeagal sheath symmetrical or not, but never bearing paraprocts; lateral lobes of aedeagus at least 7/8 length of median lobe; apices sometimes visible ventrally . . . 3
3. Posterolateral angles of pronotum acute, lateral margins subparallel (Fig. 19A,C-E); elytral interstitial lines poorly defined (except in *L. cowleyi*); head never completely concealed by pronotum at rest; posterior half of aedeagal sheath sternite symmetrical, anterior prolongation of sheath sternite narrowly tapered; (Fig. 21C-H); aedeagus either: elongate slender, median lobe slightly longer than apices of lateral lobes which are not visible ventrally (Fig. 21O-W), or aedeagus with median lobe much shorter than lateral lobes which are broad in their basal 1/2 and narrowed in their apical 1/2 (Fig. 21K), or aedeagus with median lobe only a little shorter than lateral lobes which are broad in their basal 3/4 and closely approximate dorsally, with their apices narrowed and widely separated in their apical 1/4 (Fig. 21L-N) . . . . *Luciola (Luciola)* Laporte
   Posterolateral angles of pronotum rounded, lateral margins diverging posteriorly except in *A. inconspicua* where they are subparallel; at least 2 elytral interstitial lines well defined; head often largely covered by pronotum at rest; posterior half of aedeagal sheath sternite asymmetrical (Fig. 21I,J), anterior prolongation broadly tapered; aedeagus with apices of lateral lobes never acutely narrowed and always visible ventrally; median lobe always slightly longer than lateral lobes (Fig. 5) . . . . *Atyphella* Olliff

Atyphella Olliff, 1890

Atyphella Olliff, 1890: 645. Lea, 1909: 110; Olivier, 1909b: lxxxii; 1910: 40; 1911a: 171; 1913: 417; McDermott, 1964: 45; Ballantyne, 1987b: 172, 175-77, 181. 183-5. Calder, 1998, 176.
Luciola (Luciola) Laporte, sensu McDermott, 1966: 99.
Luciola (Atyphella) (Olliff). Ballantyne, 1968: 108. Ballantyne & McLean, 1970: 236.

TYPE SPECIES. *Atyphella lychnus* Olliff, 1890, designated by Wittmer, 1958.

DESCRIPTION. MALE. This treatment extends Ballantyne & McLean (1970). Dorsal surfaces more or less conspicuously punctate, and moderately pubescent.

Pronotum. Width/length 1.5-2.6, always wider than long; usually wider across posterior third than anterior third; midanterior margin rounded, often projecting beyond obtusely rounded anterolateral corners; lateral areas explanate (Fig. 2A,C,D,F,H,I) usually more widely so in posterior half; if viewed from above lateral margins usually divergent posteriorly at least in anterior half (Fig. 1); posterolateral corners rounded, usually obtusely.

Elytra. Punctation not larger than pronotal punctures; lacking deflexed apex; interstitial lines 1, 2 always moderately prominent; sutural and epipleural margins continuous to apex which is rounded.

Head. When viewed from above is either completely or partially covered in withdrawn condition by the pronotum (Figs 1, 2); vertex moderately to deeply depressed; posterolateral eye excavation present but not visible when head is retracted; GHW 6-13 × SIW; labrum small, not much broader than long, anterior margin curved; antennal sockets close, often contiguous, antennae never separated by more than 1.5 × ASW; frons-vertex junction often well defined and may be acute (Fig. 2C,F,G,I); eyes closely approaching ventrally. Mouthparts small, (Fig. 2), often feebly developed (Fig. 2I), apical segment of labial palpi fusiform or flattened and dentate along inner margin.

Antennae. Length slightly < GHW to slightly < 2× GHW; segments simple, usually 11, sometimes less, FS1 longer than pedicel; at least some FS not much longer than wide; apical FS never conspicuously shortened and club-like, no FS produced laterally or flattened.

Legs. All femora and tibiae straight, no femora or tibiae curved or swollen. MFC absent.

Abdomen. Posterior margin of basal abdominal sternites straight. Light organs occupying sternite 6 completely and entire in 7 although sometimes retracted to anterior half (Figs 3, 4); any slight retraction of the light organ material from the lateral margins is probably a post-mortem change. Sternite 7 MPP apically rounded, less than twice as long as wide, not upturned or engulfed by the downturned apex of tergite 8; posterolateral areas rounded but not produced; posterior margin lacking incurving lobes, pointed projections, median carina, median longitudinal trough and dimple; median posterior area not swollen or arched. Tergite 8 symmetrical, not conspicuously shortened, nor projecting conspicuously beyond the apex of the MPP of sternite 7, not downturned at its apex nor engulfing the apex of sternite 7; not heavily sclerotised; rounded posteriorly with median posterior margin gently emarginate and lateral margins subparallel; ventral surface lacking flanges, lateral troughs or elevated ridges; pale coloured.

Aedeagal sheath. (Fig. 21I,J) about 3 times longer than broad; anterior half of sternite moderately broad and symmetrical, posterior half asymmetrical; tergite lacking lateral protuberances and anterior margin evenly emarginate. Aedeagus length/width 1.8-3.5, symmetrical; ML not much longer than LL; LL separated by > half their length, lacking fleshy or strap like lobes at mid-point of their inner ventral surface; LL tapering to their apices and divergent at least in apical 1/6, and visible from below; basal piece lacking accessory appendages (Fig. 5).

FEMALE. Macropterous; or elytra fully developed with hind wings shortened or absent; or elytra about as long as pronotum, meeting in midline, and hind wings abbreviated; or elytra about half as long as pronotum, usually not contiguous in midline, and hind wings minute vestiges or absent (Fig. 6C).

Pronotum. Rounded anterior margin and usually subparallel-sided in brachelytral females (Fig. 6C); pronotal outline of macropterous females as for male (Fig. 6A,B).

Elytra. Interstitial lines present on all but very abbreviated elytra.

Head. Small, shallowly excavated between eyes, often concealed beneath pronotum when withdrawn in flightless females; GHW at least 2 × SIW in brachelytral females; eyes of macropterous females moderately reduced compared to male (Fig. 6B); eyes of brachelytral females considerably reduced (Fig. 6D,E).

Light Organ. Occupying sternite 6 only; sternite 8 tapering posteriorly (Fig. 6F-H).

LARVA. Tergal margins (except for terminal tergum) laterally explanate (Figs 7, 12, 15); tarsal claw 1/6 as long as tibiotarsus; all abdominal terga subequal in length and about half median length of thoracic tergum 3; otherwise as described for the genus *Luciola*.

REMARKS. Olliff (1890) described *Atyphella* from 3 new Australian species and included the first descriptions of an Australian lampyrid female and larva. Lea (1909) doubted the distinctiveness of *Atyphella* (based on the shape of the terminal abdominal segments in the male). Olivier (1909b) retained *Atyphella* because of its distinct 'facies' and restricted distribution. McDermott (1964) did not consider *Atyphella* a valid grouping and formally incorporated it into *Luciola* (1966). Ballantyne (1968) and Ballantyne & McLean (1970) treated *Atyphella* as a subgenus of *Luciola*; Ballantyne (in Calder, 1998) restored it to generic level based on 7 Australian species including *majuscula* (Lea) which was transferred from *Luciola*. The phylogenetic analysis performed subsequently supports an *Atyphella* clade and distinguishes 22 species, which are assigned here.

Olliff's (1890) incorrect assignment of *Atyphella* to the Lampyrinae because of the concealed head of the male, (while correctly assigning other Australian Lampyridae to the Luciolinae), may have led Lea and others to question its validity. Olivier's catalogues of 1902 and 1907 did not include *Atyphella*, which he first included, in the Luciolinae, in 1910.

Sixteen species were described originally as *Atyphella*, or reassigned subsequently. *Atyphella* is now considered to include the following 22 species including 6 new species, 7 non Australian species and 6 which were originally described as *Luciola* species.

Australian species: *atra* Lea; *brevis* Lea; *conspicua* sp. nov.; *costata* (Lea) gen. rev.; *ellioti* sp. nov.; *flammans* Olliff; *flammulans* sp. nov.; *immaculata* sp. nov.; *inconspicua* (Lea); *lewisi* sp. nov.; *lychnus* Olliff; *majuscula* (Lea); *olivieri* Lea; *scintillans* Olliff; *similis* sp. nov.

Non Australian species assigned here to *Atyphella*: *aphrogeneia* (Ballantyne); *carolinae* Olivier; *huonensis* (Ballantyne); *leucura* Olivier; *marginipennis* (Guérin); *obsoleta* Olivier; *wolfi* (Olivier).

The remaining 7 species originally assigned to *Atyphella* are not Australian and need further investigation. Four are not well represented in collections: *Luciola ignota* (Olivier) may simply be a pale variety of *A. obsoleta* Olivier; *L. messoria* (Olivier) and *L. scabra* (Olivier) are difficult to reliably identify in collections; *L. testaceolineata* (Pic) has an incomplete type and its similarities to the *flammans* – *flammulans* complex need to be investigated.

Ballantyne (1968) erected *Pygatyphella* as a subgenus of *Luciola*; it was distinguished by its distinctive abdominal modifications but named for its similarities to *Atyphella*. This study transfers to *Atyphella* two species of *Luciola* (*Pygatyphella*) (viz. *obsoleta* Olivier and *huonensis* Ballantyne) and all species of this subgenus should be investigated. Of the other species, *A. peculiaris* Olivier was assigned to *Luciola* subgenus *Pygatyphella* (Ballantyne, 1968). The position of *L. salomonis* Olivier is uncertain (Ballantyne, 1992).

Species groups in the following key are those identified by cladistic analysis and defined in Table 1.

KEY TO SPECIES OF *ATYPHELLA* MALES FROM AUSTRALIA

1. Pronotum yellow or cream with no darker markings . . . 2

Pronotum always with at least a median dark area on disc . . . 4

2. Dorsal surface orange yellow except for black apical 1/5 of elytra . . . *costata* (Lea)

Dorsal surface of pronotum yellow; elytra entirely black . . . 3

3. Large (10.7-13.4mm long); elytra convex-sided when closed and bearing 4 well defined interstitial lines; lateral lobes of aedeagus closely approximate dorsally for most of their length (Fig. 5A-C) . . . *majuscula* (Lea)

Smaller (7-9mm long); elytra parallel-sided when closed, and bearing 3 well defined interstitial lines; lateral lobes of aedeagus divergent along their length dorsally (Fig. 5M-O) . . . *immaculata* sp. nov.

4. Often very small (less than 4mm long); only 2 well defined interstitial lines (1, 2) present on elytra; if line 4 present it is ill defined and often effaced posteriorly . . . 5

Never less than 6mm long; elytra always with at least 3 well defined interstitial lines . . . 6

5. Pronotum cream with a median dark marking, pronotal margins always paler than rest; abdominal tergites 6 and 7 pale brown; light organs in sternite 7 appearing as 2 compact lateral areas closely adpressed to the sternite, with irregular less compact material between (Fig 4H) . . . *lewisi* sp. nov.

Pronotum moderately dark brown, margins not paler than rest; abdominal tergites 6 and 7 very dark brown, almost black; light organs in sternite 7 entire (Fig. 3C) . . . *ellioti* sp. nov.

6. Elytra with 4 well defined interstitial lines of which line 3 is almost as long as lines 1, 2, or if shorter it is not effaced anteriorly . . . 7

Elytra with at most 3 well defined interstitial lines present (1, 2, 4) of approximately equal length; if line 3 is present then it is not as well defined and is shorter than rest and effaced in front and behind . . . 9

7. Elytra black, interstitial lines and margins not paler than rest . . . *scintillans* Olliff

Elytra pale to moderately dark brown, margins and/or interstitial lines often paler than rest . . . 8

8. Elytra dark brown with lateral, apical and sutural margins pale; interstitial lines 1-3 not paler than rest . . . *olivieri* Lea

Elytra light to moderate brown; margins and interstitial lines usually slightly paler than rest . . . *lychnus* Olliff

9. Elytra moderate to dark brown, lateral margins and interstitial lines no paler than remainder . . . 10

Elytra pale to dark brown, interstitial lines and sometimes also margins paler than rest . . . 12

10. Pronotum sub-parallel-sided (Fig. 1E); head large, not completely concealed from above; mouthparts well developed . . . *inconspicua* (Lea)

Lateral pronotal margins diverging posteriorly (e.g. Fig. 1A,F,J); head smaller, concealed from above; mouthparts not well developed . . . 11

11. Elytra convex sided when closed; frons-vertex junction convex; antennal sockets not contiguous (Fig. 2A, B) . . . *monteithi* sp. nov.

Elytra parallel-sided when closed; frons-vertex junction acute; antennal sockets contiguous (Fig. 2I) . . . *atra* Lea

12. Medium to large (8-13mm long); elytra with 4 interstitial lines of which 3 is more faintly defined and always shorter than rest; all interstitial lines pale; frons-vertex junction ill defined, convex . . . *flammans* Olliff

Smaller; elytra with at most 3 interstitial lines which may be paler than rest or not; frons-vertex junction well defined, acute . . . 13

13. Antennal sockets not contiguous . . . 14

Antennal sockets contiguous or very close . . . 16

14. Frons-vertex junction with median area slightly elevated (Fig. 2F,G); antennal sockets separated by slightly greater than their width . . . *conspicua* sp. nov.

Frons-vertex junction not elevated in median area; antennal sockets separated by < their width (Fig. 2C) . . . 15

15. Pronotum with lateral margins divergent at least in anterior half (Fig. 1I) . . . *similis* sp. nov.

Pronotum with lateral margins subparallel (Fig. 1E) . . . *inconspicua* (Lea)

16. Pronotum moderately dark brown, margins may be narrowly paler; mouthparts feebly developed; elytra either entirely medium brown with interstitial lines no paler than rest, or interstitial lines and lateral margins narrowly paler; elytra parallel sided when closed, only known from RF in SE Qld . . . *atra* Lea

Pronotum cream with dark markings restricted to median area; mouthparts feebly to moderately developed; elytra never entirely medium brown, always with lateral margins and interstitial lines paler than rest; elytra slightly convex sided when closed; known only from RF in far NE Qld . . . 17

17. Elytra pale, often semitransparent such that body outlines or hind wings may be visible through cuticle; frons 2-3 × ASW . . . *brevis* Lea

Elytra not semitransparent, hind wings not visible, although fat body material beneath cuticle may be apparent; frons high, 5-6 × ASW . . . *flammulans* sp. nov.

KEY TO KNOWN FEMALES OF AUSTRALIAN *ATYPHELLA*

1. Elytra and hind wings fully developed; elytra usually cover gravid abdomen and female assumed capable of flight . . . 2

Female brachelytral; if elytra cover abdomen then hind wings are shortened or absent and female is flightless . . . 3

2. Elytra uniformly dark brown . . . *majuscula* (Lea)

Elytra orange yellow with black apices . . . *costata* (Lea)

3. Elytra either cover whole body or at most 2-3 abdominal segments visible beyond elytral apices . . . 4

Elytra cover less than 1/3 of abdomen (Fig. 6C) . . . 7

4. Elytra fully developed; hind wings shortened but always at least half as long as elytra . . . 5

Elytra fully developed but may not cover gravid abdomen entirely; hind wings vestigial or absent . . . 6

5. Hind wings almost as long as elytra; elytra dark brown with wide pale margins; interstitial lines no paler than rest . . . . *olivieri* Lea

   Hind wings about 2/3 as long as elytra; elytra pale brown with margins and interstitial lines paler than rest . . . . *flammans* Olliff

6. Elytra with 4 well defined interstitial lines . . . . *lychnus* Olliff

   Elytra with 3 well defined interstitial lines (1, 2 and 4) . . . . *atra* Lea

7. Elytra at least half as long as pronotum and contiguous in median line when abdomen is gravid . . . . *scintillans* Olliff

   Elytra less than half as long as pronotum; sometimes contiguous in median line (Fig. 6C) 8

8. Elytra present as narrow lateral strips . . . *lewisi* sp. nov.

   Elytra about as long as wide 9

9. Pronotum smooth, shiny, with punctures separated by 1-2 times their width; posterolateral corners of pronotum not projecting . . . . . *similis* sp. nov. & *conspicua* sp. nov.

   Pronotum not markedly smooth or shiny; punctures contiguous; posterolateral corners of pronotum projecting (Fig. 6C) . . . . *inconspicua* (Lea)

KEY TO KNOWN LARVAE OF AUSTRALIAN *ATYPHELLA*

1. Protergum bearing tubercles (Fig. 15A, C) 2

   Protergum lacking tubercles (Fig. 7A, Fig. 12, Fig. 15B) 3

2. Lateral margins of terga strongly ridged; punctures on anterior of terga 2-11 not large or conspicuous; dorsal colour pattern as in Fig. 15A . . . . *olivieri* Lea

   Lateral margins of terga not strongly ridged; punctures on anterior of terga 2-11 large and conspicuous; dorsal colour pattern as in Fig. 15C . . . . . . *scintillans* Olliff

3. Posterolateral margins of protergum acute (Fig. 12C) . . . . *majuscula* (Lea)

   Posterolateral margins of protergum rounded 4

4. Terga 2-3 darker than remainder (Fig. 7A, Fig. 12A) . . 5

   Terga 2-3 not darker than remainder (Fig. 12B, 15B) 6

5. Protergum dark brown with dark margins (Fig. 7A) . . . . *atra* Lea

   Protergum pale with darker markings, margins pale (Fig. 12A) . . . . *flammans* Olliff

6. Dorsal colour moderately dark brown and yellow; no paler markings adjacent to median line in segments 2-9 (Fig. 15B) . . . . *lychnus* Olliff

   Dorsal colour pale brown and cream (Fig. 12B); paler markings adjacent to midline on at least segments 2-7 . . . . *similis* sp. nov.

Atyphella atra Lea, 1921
(Figs 1, 2, 3, 7, 8)

Atyphella atra Lea, 1921a: 198. Ballantyne in Calder, 1998: 177 (comb. rev.).

Luciola (Luciola) atra (Lea). McDermott, 1966: 99.

Luciola (Atyphella) atra (Lea). Ballantyne & McLean, 1970: 281, figs 4a, b. Moore, 1989: 136.

TYPES. Holotype ♂, Australia, S Qld, 28.19S, 153.05E, Lamington NP (C2290, QM). Of 2♂ specimens on card, holotype indicated by 'TY'. Paratypes, 10♂ same locality as holotype, xi. 1920, HH, labelled as 'National Park, Queensland' (1 QM; 4 SAM; 1 MV; 2 BMNH; 2 ANIC).

MATERIAL. Holotype, 10 paratypes and 89 specimens. S QLD: 26.44S, 152.43E, Conondale, 29.xi.1974 (sites 12-13), GBM, 7♂ (UQ). 27.20S, 152.46E, Maiala NP, Mt. Glorious; 21.xi.1964, LP, 15♂, 6♀, 5 larvae, eggs (T. 91-93, 110-112, 154); 20.vi.1965, A. Jones, 1 larva (T.152), 6.30 p.m., 6.xi.1964, LP, 3♂ (T.95), 1♀ (T.94). Mt Glorious, nr Maiala NP, 1.xii.1966, GBM, S. Curtis, A. May, 37♂; x.1965, B. Ingram, 1 larva (T.153); 2♂ (QM). Lamington NP, xi. 1920, HH, 8♂ (QM, MV). NE NSW: 28.51S, 152.56E, Wiangaree SF, Antarctic Beach (sic), 13.xii.1986, V. R. Bejsak, 2♂, 1♀ (MM).

DIAGNOSIS. Male small to medium (5.4-7.0mm long); pronotum brown (margins may be paler); elytra light brown often with the 3 interstitial lines (1, 2, 4) and lateral margins slightly paler; elytra parallel-sided when closed; antennal sockets contiguous; mouthparts small, non functional; frons-vertex junction acute (Fig. 2I). Female dingy cream; elytra fully developed, hind wings vestigial. Larva (Fig. 7A) with dark brown thoracic terga having few paler markings; abdominal terga cream with scattered dark markings.

DESCRIPTION. Males are redescribed; females and larvae are newly described.

Male. 5.4-7.0mm long (holotype 7.0mm long); pronotum dusky brown, sometimes with anterior and lateral margins narrowly paler, and darker brown markings anteriorly on disc; pronotal punctures often narrowly ringed with brown or black; MS cream or dingy cream, sometimes brown in posterior half; MN dingy cream; elytra shiny, light - moderately brown, three interstitial lines and lateral margins sometimes paler; head and antennae very dark brown; ventral surface of pro and mesothorax light brown, of metathorax dark brown; legs pale brown, femora sometimes paler than rest; ventral abdomen black except for white sternites 6, 7; dorsal abdomen dark brown except for pale cream tergites 7 & 8.

Pronotum (Fig. 1A) 1.7-2.5mm wide; 0.9-1.4mm long, W/L (holotype) 2.0; midanterior margin broadly rounded or straight, and produced a little, if at all, beyond anterolateral angles; anterior margin sometimes reflexed; lateral margins diverging posteriorly; median posterior margin indented or not; disc fairly flat, irregularly depressed, posterolateral ridge pronounced; punctures broad, shallow, contiguous, not all the same size. Elytra parallel sided, with 3 interstitial lines (1, 2, 4) of which 1 & 2 are well defined.

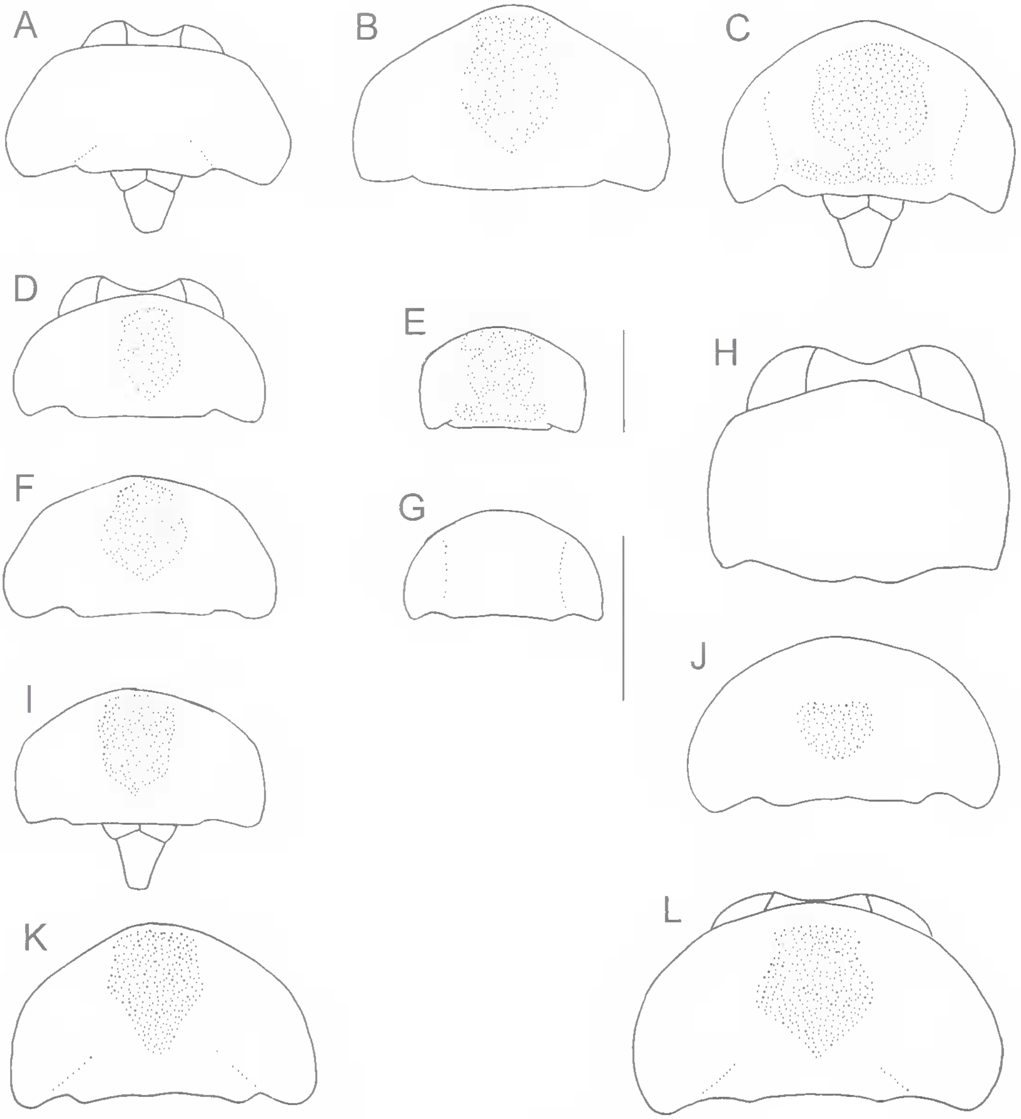

FIG. 1. Dorsal views of pronota of ♂ *Atyphella*; stippling indicates extent of colour pattern; A, D, H, L, show exposed head. A, *Atyphella atra* holotype; B, *A. conspicua*; C, *A. scintillans*; D, *A. brevis*; E, *A. inconspicua*; F, *A. olivieri*; G, *A. ellioti*; H, *A. costata*; I, *A. similis*; J, *A. monteithi*; K, *A. flammulans*; L, *A. flammans*. Scale lines 1mm; all but G share upper scale.

Head (Fig. 1A, 2I) almost concealed beneath pronotum at rest; deeply depressed between eyes; GHW 0.8-1.3mm; SIW 0.1mm; antennal sockets contiguous; frons high and flat, about 2 × ASW, frons-vertex junction acutely margined; mouthpart complex very small, non functional; apical segment of labial palpi fusiform. Antennal length subequal to GHW; antennal FS 1 acutely narrowed basally, 1.5 × as long as FS 2; FS 2-8 subequal, half length of FS 1, about as long as broad; FS 9 slender, longer than FS 8.

Light organs occupying sternites 6 & 7 entirely except sometimes for a narrow posterior margin of 7; (Fig. 3A); MPP of sternite 7 moderately

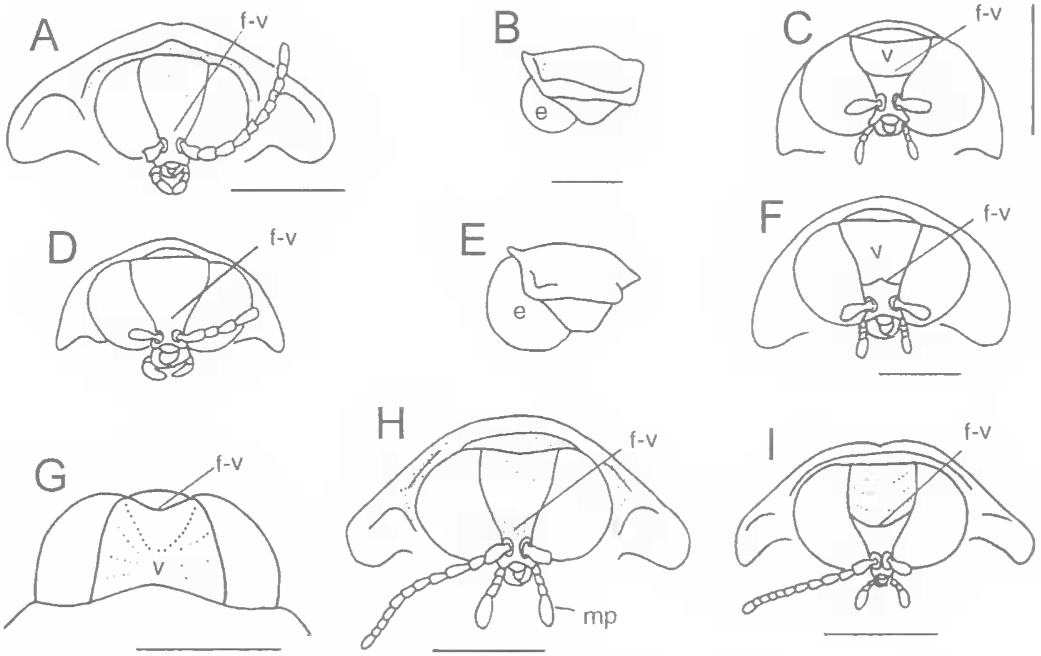

FIG. 2. Head and pronota, ♂ *Atyphella*; anterior aspects show part or all of one antenna only; lateral aspects show pronotum and extent of eye only. A, B, *A. monteithi*; C, *A. inconspicua*; D, E, *A. costata*; F, G, *A. conspicua*; H, *A. olivieri*; I, *A. atra*. Scale lines 1mm; lines shared by: B-E. e = eye; f-v = frons vertex junction, mp = maxillary palp, v = vertex.

produced and apically rounded; tergite 8 with lateral margins subparallel and median posterior margin gently produced. Aedeagus L/W 2.3; basal piece not hood like; ML slightly expanded around EO; not bulbous at apex, and not produced dorsally; LL narrowing slightly in apical 1/3, and divergent along their length in median line; hairs along lateral margins of LL in apical 1/3.

Female. 4.3-6.0mm long; with fully developed elytra, hind wings represented by minute vestiges. Dorsal body may be entirely pale cream or pale brown with no darker markings; or pronotum with median brown markings, MN dark margined and basal third of elytra slightly darker than rest; head cream - pale brown, eyes red - brown; antennae uniformly brown, or basal segments dark brown, and apical segments pale; legs brown, hind coxae dark brown; ventral surface of thorax dingy cream; abdomen pale cream; ventral surface may be orange yellow in older specimens.

Pronotal outline like male but midanterior margin indented and projecting anteriorly beyond rounded anterolateral angles; punctures broad, shallow, contiguous in lateral areas of disc, separated puncture width in middle of disc. Elytra convex-sided when closed, with 3 well-defined interstitial lines (1, 3 and 4). Head form of wingless female head type (Fig. 6E). Last 2 segments of abdomen of gravid female protrude beyond end of elytra; light organ may be retracted from all margins in sternite 7; posterior margin of sternite 8 broadly and shallowly emarginate, sternite 9 narrowing posteriorly and median posterior margin entire or slightly emarginate.

Larva. (Fig. 7A). Lateral margins of terga 1-11 covered in fine short hairs and spines, not conspicuously ridged; median line on terga 1-11 not laterally ridged; punctures in anterior half of terga 2-10 not obviously larger than rest. Protergum 1.2-1.4mm long; 1.7-2.3mm wide; median anterior area of protergum narrowing slightly; median anterior margin of protergum indented, lacking tubercles. Posterolateral corners of thoracic and abdominal terga rounded; posterolateral corners of terminal abdominal tergum not produced. Head elongate slender,

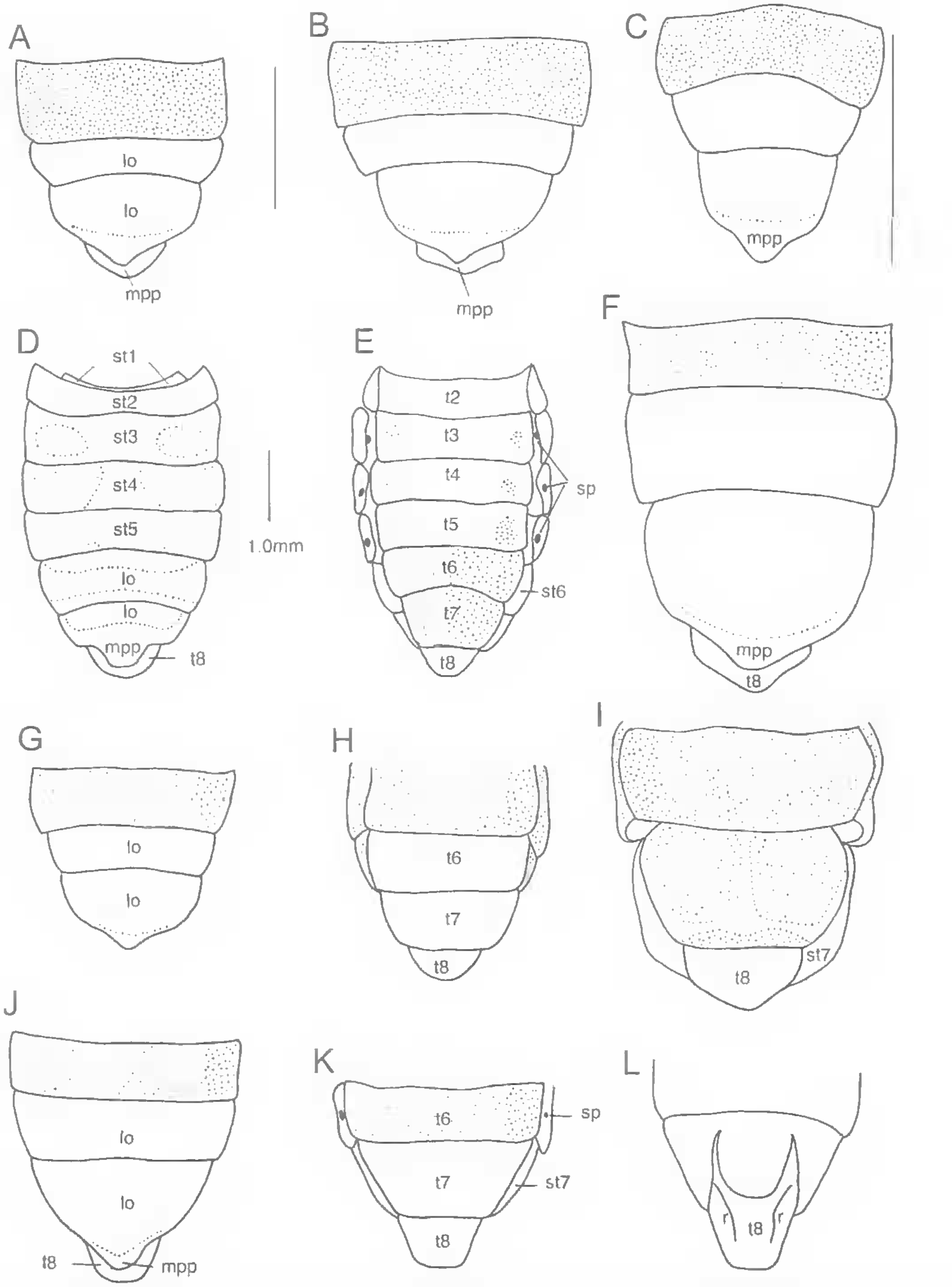

FIG. 3. Terminal abdomen, ♂ *Atyphella*; A-D, F-H, J-L, ventral aspect of abdominal sternites; E, I, K, dorsal aspect of abdominal tergites; L, ventral aspect of abdominal tergites. A, *A. atra*; B, *A. brevis*; C, *A ellioti*; D,E, *A. costata;* F, I, *A. olivieri*; G, H, *A. inconspicua*; J-L, *A. majuscula*. Scale lines 1mm; lines shared by: A, B & F-I; D, E & J-L. lo = light organ; mpp = median posterior projection sternite 7; sp = spiracle; st1-7 = sternites 1-7; t2-8 = tergites 2-8; r = ridge.

twice as long as wide; median anterior margin broadly emarginate.

Thoracic terga dark brown, with a median posterior pale area on terga 1-3; protergum with paired anterior, lateral and posterolateral pale markings; mesotergum and metatergum with paired lateral and midposterolateral pale areas; metatergum with irregular cream areas along anterior margin to each side of midline. Abdominal terga 4-9 dingy cream, with midlateral brown markings being more pronounced on terga 7-9; terga 10, 11 cream, 12 dark brown. Ventral surface of lateral expansions of thoracic plates dark brown with median cream areas; legs uniformly brown; median thoracic sternal plates scarcely differentiated; ventral surface of lateral expansions of terga on abdominal segments 4-9 pale; ventral surface of abdominal segments 4,5 including sternum and epipleural plates marked extensively in brown; ventral surface of abdominal segments 6-8 mainly cream with some brown markings; epipleural plates of segment 9 mostly dark brown; segments 10-12 cream with scarce dark markings.

DISTRIBUTION. Known from three disjunct mountain rainforest systems: the Lamington Plateau (including Wiangaree) on the Qld/NSW border, and the D'Aguilar and Conondale Ranges, respectively 40 and 90km NNW of Brisbane (Fig. 8).

REMARKS. Lea (1921a) considered this species 'close to *Atyphella brevis* and *A. olivieri*', and recorded the colour as black; neither the type specimen nor more recently collected males have such a dark dorsal colouration.

One of the females taken at Maiala NP in November 1964 (in UQ) deposited eggs. The elytra were parted, the abdomen curved dorsally, and the individual egg held for some time between the styli before being deposited. These eggs are 0.5-0.6mm across, round, cream, soft, unsculptured. Luminosity was not observed. This species and *A. lychnus* were taken together at the Conondale site.

Atyphella brevis Lea, 1909
(Figs 1, 3, 9)

Atyphella brevis Lea, 1909: 111, fig. 103; 1921a: 197; 1929: 345. Olivier, 1910: 46. Tillyard, 1926: 212, fig. R43. Ballantyne in Calder, 1998: 177 (comb. rev).

Luciola (Luciola) brevis (Lea) McDermott, 1966: 100.

TYPES. Lectotype.♂ Australia, N Qld: 17.16S, 145.29E, Atherton, (SAM). Of three♂ syntypes glued onto card the lectotype is indicated with 'TY; labels are: 1. *brevis* (handwritten), Lea Type (printed), Atherton (handwritten), 2. Handwritten label, '*Atyphella brevis* 8729 Lea Queensland' with 'type' handwritten in red at end of label. Paralectotypes. 2♂ on same card as lectotype. These 3 specimens are all that remain of the original 12 syntype series.

MATERIAL. Lectotype, 2 paralectotypes, and 146 specimens. N QLD: 5♂, H. Peters, 2♂, A. Feynes (CAS); 12♂ (QM); 2♂ E. Ferguson (ANIC). 15.43S, 145.17E, Big Tableland, NE cnr, 800m, ANZSES exp., 20.xii.1990-8.i.1991, FIT and PF traps, 1♂ (QM). 15.52S, 145.14E, Mt Misery summit, 850m, Qld Mus & ANZSES FIT site 3, 6.xii.1990-17.i.1991, 2 ♂. 15.57S, 145.08E, Mt Boolbun Sth, 850-1000m, 4-6.xi.1995, GBM, 10♂ 16.03S, 145.23E, Mt Halcyon, 870m, 22-24.xi.1993, GBM, 7♂ 16.04S, 145.25E, Roaring Meg Valley. 680m, GBM, 7♂ 20-22.xi.1993, 2♂ 7-9.xii.1993. 16.06S, 145.20E, McDowell Ra. 17km N of Daintree, 27.xi.1985, in RF, sieved litter at 520m, QM berlesate 684, 2♂. 16.30S, 145.19E, Mt Demi summit, 1100m, FIT, 17.xii.1996-25.i.1996, GBM et al., 1♂. 16.49S, 145.38E, Kuranda, G. Bryant, 13.xi.1909, 1♂. (BPBM). Mt Formantines, 10km N of Kuranda, 700m, 23-24.xi.1990, GBM et al., 12♂ (QM). 16.55S, 145.46E, Cairns, E. Allen, 1♂; J. Anderson, 2♂. 17.02S, 145.37E, Davies Ck, (15 road km from Kennedy Hwy, 21km E by S of Mareeba), 1.iii.1988, D. Rentz, stop A-28, 28♂ (ANIC). 17.03S, 145.41E, Upper Isley Ck, 750m, 29-30.xi.1993, Cook et al., 3♂ (QM). 17.06S. 145.36E, Mt Haig, 1150m, 1.xii.1994-3.i.1995, PZ, 6♂ malaise trap; 4 ♂ FIT ANIC; 2 males FIT JCU (west); 1♂ FIT JCU (east) (ANIC). 17.12S, 145.51E, Bellenden Ker Ra., Cable Tower 3, 1054 m, 17.x-5.xi.1981, Earthwatch/Q Museum. malaise trap, RF, 1♂ (ANIC Voucher 83-0670). 17.16S, 145.29E, Atherton, 7.i.1966, P. Twine, 1♂ (UQ); 4♂ (MV); 1♂ (AM). Ringrose NP via Atherton, 9.xii.1966, BC, 1♂ (T.218 UQ). Lake Barrine, Deane, 4♂. 17.23S, 145.23E, The Crater, nr Herberton, xii.1961. DKM, 2♂ (AM). 17.28S, 145.29E, Longlands Gap, BS1, 1150m, 1.xii.1994-3.i.1995, PZ, FIT, 2♂ (ANIC). 17.31S, 145.37E, Millaa Millaa Falls, 9.i.1964, 1♂ (UQ). 17.36S, 145.45E, Henrietta Ck, Palmerston NP, GBM, 20♂, 29.xi.1964, 3♂ 23.iv. 1970; 4♂29.xii.1964 (T.130), 6.xii.1965 7♂ (T.186); 12.xii.1966, BC, 1♂ (T.216); 2♂ (QM). 17.37S,145.34E, Massey Ck, 1000m, BS3, 1.xii.1994-3.i.1995, PZ, FIT, 1♂ (ANIC). Tully Falls SF, 9.5km SSW of Ravenshoe, 9.ii-3.iii.1988, RS & Dickinson, MDPI FIT 29/4, 3♂ (DPI).

DIAGNOSIS. Male small to medium (5.5-7.0mm long); pronotum cream with median dark marking; elytra slightly convex sided when closed, light to medium brown, with suture, lateral margin and the 3 interstitial lines paler; elytra semitransparent with hind wings usually visible beneath; antennal sockets contiguous or nearly so; mouthparts poorly developed; frons-vertex junction acutely margined. Female and larva not associated.

DESCRIPTION. *Male*. 5.5-7.0mm long (lectotype 5.9); pronotum cream with median dark brown markings (Fig. 1D); MS usually cream, sometimes dingy brown, MN cream; elytra semitransparent such that hind wings are often visible beneath cuticle; elytra pale to medium brown with interstitial lines cream, and all margins except for base narrowly cream; a faint pale line may exist in the position of interstitial line 2; elytra sometimes very pale, scarcely any darker than interstitial lines; head very dark brown, antennae lighter brown; ventral thorax cream except for dark brown metathorax, hind coxae, and tibiae and tarsi of all legs; ventral abdomen dark brown except for pale cream sternites 6 & 7; dorsal abdomen dark brown except for pale tergites 7 & 8.

Pronotum (Fig. 1D) 1.9-2.3mm wide; 1-1.2mm long; W/L (lectotype) 1.8; midanterior margin bluntly rounded, usually produced beyond anterolateral angles; lateral margins slightly divergent posteriorly; punctures close, but not all contiguous. Elytra slightly convex sided when closed, with 3 well defined interstitial lines (1, 2, 4) and sometimes traces of line 3, which is feebly developed, effaced in front and behind and not margined by punctures.

Head almost concealed beneath pronotum at rest; deeply depressed between the eyes; GHW 1.2-1.6mm; StW 0.1-0.2mm; ASD < ASW, sockets contiguous or nearly so; frons high, at least 2 × ASW, frons-vertex junction acutely margined; mouthparts small; apical segment of labial palpi entire. Antennal length subequal to GHW; FS 1 narrowed basally, slightly longer than 2, which is slightly longer than 3; FS 4-8 subequal, about as long as wide.

Light organs (Fig. 3B) occupying sternites 6 & 7 except for narrow to moderately wide band across posterior margin of 7; MPP of sternite 7 moderately produced and apically rounded; lateral margins of tergite 8 subparallel; mid-posterior margin rounded and projecting beyond rounded posterolateral corners. Aedeagus L/W 2.3; basal piece not conspicuous and hood-like; ML slightly bulbous at apex and at the level of the EO, not projecting dorsally; LL subparallel-sided, broad at apex, very close in dorsal aspect, and separating only in apical 1/3: hairs along lateral margins of LL in apical 1/3.

DISTRIBUTION. Widespread in mountain rainforest of the Wet Tropics zone of N Qld from just south of Cooktown to a little south of Ravenshoe. Altitude records range from 400-1160m, with the exception of an early record from sea level at Cairns which is probably inaccurate (Fig 9).

REMARKS. Lea (1909) recorded this species as close to some *A. lychnus* but he may have confused some specimens. He considered that *A. brevis* and *Luciola cowleyi* 'might fairly be regarded as linking *Atyphella* and *Luciola* together'. There is only a superficial colour similarity (Ballantyne, 1968) between these very different species. Lea (1921a) considered that the female of *brevis* was unknown, but indicated at least one Queensland species (not named) had larva-like females; subsequently Lea (1929) recorded 2 males of *A. brevis* and 2 larva-like forms, 'possibly females' of *brevis* (from Lamington NP, in QM). The males are *Atyphella similis* sp. nov. and the larvae *A. scintillans*. E. Allen's personal copy of Lea's 1909 paper, from the Entomological Society of Queensland library, has a pencilled notation by Allen on page 111, against the description of *brevis*: 'discovered later in my excursions that the females are wingless and remained on the ground where the males found them'. I have not been able to associate females with this species.

Tillyard (1926: 212, fig. R43) inaccurately shows *A. brevis* male with 3 instead of 2 sternites containing the light organ.

Atyphella conspicua Ballantyne sp. nov.
(Figs 1, 2, 10)

TYPE. Holotype.♂, 16.42S, 145.13E, Stewart Ck, 4km NNE Mt Spurgeon, camp 2, 1200-1250m, 17-19.x.1991, GBM, HJ, DC & Roberts (QMT61017, QM).

MATERIAL. Holotype and 94 paratypes. N QLD: 15.42S, 145.13E, Mt Finnigan summit via Helenvale, 28-30.xi.1985, 1100m, PF traps, RF, GBM, DC, 2♂; Mt Finnigan, 760m, 20-27.vii.1974, GBM, DC, 1♂ (QM). 16.10S, 145.23E, Thornton Peak via Daintree, 1000-1300m, 20-22.ix.1981, GBM, DC, 4♀. 16.28S, 145.23E, nr plane crash site 11km NW of Mossman, 27.xii.1989, 1240m, ANZSES, 2♂. Carbine Tbld, plane crash site, 27-28.xi.1990, 1330m, PF traps and hand. GBM, 22♂. Carbine Tbld, above Fern Patch, Devil's Thumb, 26-27.xi.1990, 1050m, PF traps, GBM, HJ, 3♂. 16.34S, 145.16E, Mt Lewis via Julatten: 2.5km N of, 3.xi.1983, DY, GT, berlesate 613, RF, sieved litter, 1♂ 26.xi.1980, RS & Titmarsh, berlesate, 1♂ (DPI); top of Mt Lewis, 27.xi.1965, GBM, 2♂ (taken with one♂ of *A. inconspicua*; T.189, UQ). 16.42S, 145.13E, Stewart Ck, 4km NNE Mt Spurgeon, camp 1, 1250-1300m, 15-20.x.1991, GBM, 18♂; camp 2, 1200-1250m, 17-19.x.1991, 30♂, 4♀ (QM). 17.36S, 145.45E, Henrietta Ck, 6.xii.1965, GBM, 2♂ (taken with 2♂ of *A. inconspicua*).

DIAGNOSIS. Males distinguished from *A. inconspicua* by the divergent lateral margins of the pronotum, the median elevation of the frons-vertex junction and relatively larger size

(7.2-9.8mm long); distinguished from *A. similis* by the shape of the frons-vertex junction, colour of terminal abdominal tergites, and its northerly distribution. Possible female brachelytral.

DESCRIPTION. *Male*. 7.2-9.8mm long; pronotum may be light brown or pale cream with median area darker brown; MS and MN pale cream; elytra light to quite dark brown, interstitial lines 3 and 4 sometimes paler brown; head between eyes very dark brown, sometimes paler brown below antennal insertions; labrum pale brown; antennae and palpi brown; ventral pro- and mesothorax and bases of legs pale yellow, apex of femora, tibiae and tarsi brown; ventral metathorax light brown; basal abdominal sternites very dark brown; light organs white; basal abdominal tergites brown, tergites 7 and 8 pale cream, posterior margin of 7 may be narrowly brown.

Pronotum (Fig. 1B) 1.6-2.8mm wide, 1.4-1.6mm long, W/L 1.7 (holotype); midanterior margin rounded and considerably produced beyond rounded anterolateral angles; lateral margins divergent posteriorly in at least anterior 2/3, often convergent in posterior 1/3 or less; punctures broad, shallow, contiguous over most of dorsal surface except in median area where punctures are smaller and small shiny apunctate areas exist. Elytra parallel-sided, with 3 interstitial lines of which 1, 2 are best defined.

Head partially concealed at rest; moderately deeply excavated between eyes; GHW 1.7-2.1mm; SIW 0.3mm; ASD subequal to or slightly > ASW; frons with transverse depression above antennal insertions and often a median longitudinal depression; frons height subequal to ASW, frons-vertex junction acutely margined and elevated in median line (elevation visible from in front, or above, or from both aspects Fig. 2F,G); mouthpart complex well developed; apical segment of labial palpi fusiform. Antennal length subequal to or slightly longer than GHW; FS 1 slightly longer and narrower than FS2; FS2 as wide as, but slightly longer than FS3; FS 4-8 subequal in length, and slightly shorter than FS3; FS9 about 1.5 times as long as FS8.

Light organs occupying sternites 6 and 7 entirely except for posterior margin of sternite 7 and sometimes also narrow lateral margins; MPP of sternite 7 moderately produced and apically rounded; tergite 8 with lateral margins subparallel and median posterior margin rounded. Aedeagus as described for *A. inconspicua*.

Female. Associated by similarity of label data only; about 8mm long (females examined are gravid and very soft); brachelytral, hind wings represented by minute vestiges. Dorsal body pale cream, semitransparent; pronotum with pale brown median marking and elytra light brown with pale interstitial lines, suture and lateral margin; light organ in sternite 7 paler than rest.

Pronotum with median anterior margin indented; anterolateral angles not distinguishable from above; lateral margins slightly divergent posteriorly along their length; posterolateral corners of pronotum not projecting; dorsal surface very smooth and shiny, punctures small, shallow, separated by 1-2 × their width. Elytra on alcohol-preserved specimens can be manipulated with forceps to touch in the median line but are not contiguous in any of the 4 females examined; with 3 well-defined interstitial lines. Head covered by pronotum at rest, of form of wingless female head type. Median posterior margin of sternite 8 broadly emarginate, of sternite 9 entire.

DISTRIBUTION. Restricted to the Wet Tropics of N Qld where all records are from high elevation (750-1300m) in mountain blocks 1, 2 and 4 except for one collection at 350m in block 14; usually the only species taken, except twice with *A. inconspicua* (Fig. 10).

REMARKS. *A. conspicua* is named for its similarity to *A. inconspicua* and its distinguishing features of larger size and more conspicuous 'facies'.

Atyphella costata (Lea) comb. nov.
(Figs 1, 2, 3, 5, 6, 8)

Luciola costata Lea, 1921b: 66.
Luciola (Luciola) costata Lea. McDermott, 1966: 102. Calder, 1998: 178.

TYPES. Holotype.♂, Australia, Northern Territory: 14.44S 131.08E, Flora River, ix. 1912, Spencer (T2876, MV). Paratype♂ same data (I12280, SAM).

MATERIAL. Holotype, 1 paratype and 62 specimens. 10.00S, 142.00E, Moa (Banks) I., at light, W. McLennan, 2♂ 17.i.1920 (SAM); 11.i.1920 8♂ (AM). NORTHERN TERRITORY: 13.49S, 136.28E, Groote Eylandt, N. Tindale, 5♂ (SAM), 2♂ (AM). 12.27S, 130.50E, Tortilla Flats via Darwin, 8.xii.1966, C. Li, 2♂ (MAGNT). 14.11S, 132.11E, Edith Falls, xii.1983, Potts, 1♂. 14.23S, 129.51E, Beebom Crossing, Daly R on Tipperary Station, 28.xi.1972, T Angeles & N Forrester, 3♂. 14.28S, 132.16E, Katherine, Maud Ck, 3.xii.1978, RS, at light, 2♂ (DPI). Katherine, 28.ii.1973, T.W. & A. Allwood, 1♂. 14.29S, 131.22E, Crocodile R nr Dorisvale, MV light, 17-18.xi.1984, M. Malipatil, 11♂. 14.30S, 132.15E, 3km

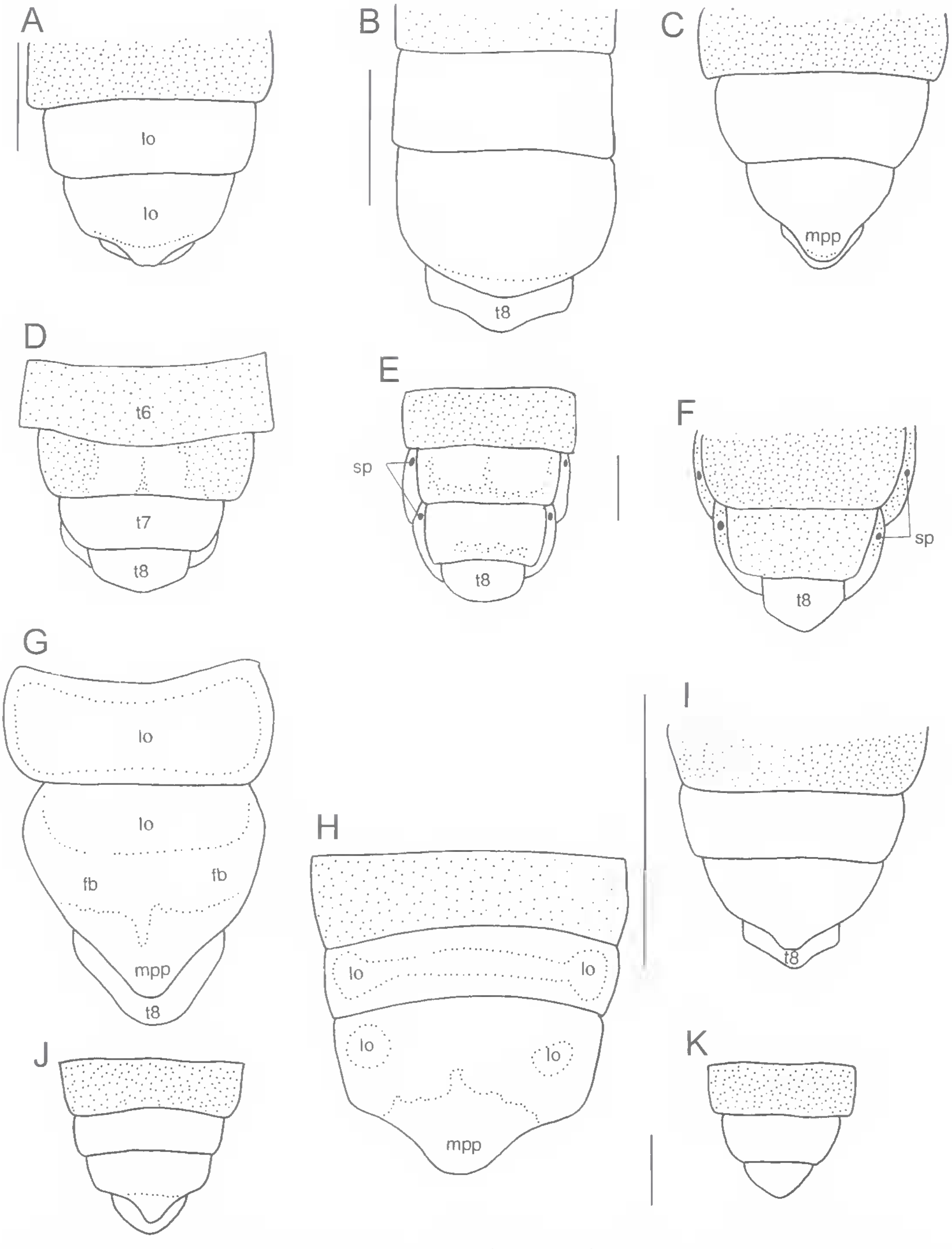

FIG. 4. Terminal abdomen, ♂ *Atyphella*; A-C, G-J, ventral aspect of abdominal sternites; D-F, K, dorsal aspect of abdominal tergites. A, D, *A. similis*; B, E, *A. immaculata*; C, F, *A. monteithi*; G, *A. flammulans*; H, *A. lewisi*; I, *A. lychnus*; J, K, *A flammans*. Scale lines 1mm; lines shared by: A, C, D, F; B, G, I; E, J, K. Abbreviations as for Fig. 3.

SSW of Katherine, 12.xi.1979, TW, 4♂ (ANIC). Katherine Gorge NP, 4-5.xii.1980, M. Malipatil, 1♂ (MAGNT). 14.31S, 132.22E, Tindal, 1-20.xii.1967, light trap, W. Vestjens, 2♂ (ANIC). 14.39S, 133.06E, Mataranka, 1.iii.1967, MU, 1♂. 14.44 S 131.08E, Flora R, ix.1912, Spencer, 3♂ (MV). 14.56S, 133.04E, Roper R crossing 2km W of Mataranka Hsd, 11.i.1992, M. & B. Moulds, 6♂ (AM). 14.57S, 133.13E, Roper R, N. B. Tindale, 1♂ (MV). 15.40S, 130.39E, Victoria R Depot, 4♂ (BMNH). N QLD: 13.01S, 141.47E, 40km S of Weipa, 1-10.xii.1987, Clarkson, DeCampo, 1♂ (DPI). 13.05S, 142.56E, Wenlock R, 12.xii.1986, M.V. lamp, G. Daniels, M. Schneider, 1♀ (UQ).

DIAGNOSIS. Male 7.7-9.7mm; one of only two Australian fireflies which are dorsally yellow with apical black patches on elytra; distinguished from *Luciola dejeani* by the dark brown abdominal sternites 4 and 5, the well developed elytral interstitial lines, and the form of the aedeagus. Female macropterous, coloured as for male except for pale terminal abdomen. Larva not associated.

DESCRIPTION. Males are redescribed; females are newly described.

Male. 7.7-9.7mm long (holotype 8.7mm long); dorsal surface yellow to orange yellow, except for apical black area on elytra; head between eyes, antennae, and palpi dark brown; ventral thorax yellow except for dark brown tibiae and tarsi of all legs; abdominal sternite 2 yellow, 3-4 yellow with lateral brown markings or 3-4 entirely dark brown; 5 dark brown, 6 and 7 creamy white; abdominal tergites brown (6 and 7 may be darker brown than preceding tergites), tergite 8 paler brown than remainder.

Pronotum (Fig. 1H) 2.5-3.2mm wide, 1.7-2.1mm long; W/L 1.5 (holotype); midanterior margin rounded, moderately produced beyond conspicuous but rounded anterolateral angles; lateral margins subparallel or slightly divergent posteriorly; median posterior margin gently indented; punctures broad, shallow, contiguous except over median area of disc. Elytra parallel-sided when closed, with interstitial lines 1, 2 well-defined, 3, 4 faint.

Head (Figs 1H, 2D,E) not completely covered by pronotum at rest, moderately excavated between eyes; GHW 1.9-2.4mm; SIW 0.2-0.4mm; ASD slightly < ASW; frons 1 × ASW, frons-vertex junction not clearly defined and rounded; mouthparts well developed; apical segment of labial palpi flattened and dentate. Antennal length > GHW but < 2 × GHW; FS 1 slightly longer than subequal FS 2, 3; FS 4-9 subequal, a little shorter than FS 2, 3.

Light organs (Fig. 3D) either occupying sternites 6 and 7 completely or retracted to basal half or less of sternite 7 (such retraction may be a post-mortem change); MPP broad and apically rounded, lateral margins convergent posteriorly; posterolateral 'corners' of sternite 7 apparent and angulate on certain pinned specimens, angles obliterated after short period of soaking in water/detergent mixture; tergite 8 rounded posteriorly (Fig. 3E). Aedeagus L/W 2-3, like that of *Atyphella majuscula* (Fig. 5G-I) but lacking the hood like basal piece; ML scarcely expanded at apex or around EO; LL subparallel sided or margins tapering slightly posteriorly; LL broad in lateral aspect and closely approximate for most of their dorsal length and diverging only at their apices; LL bear a small subapical hook, and hairs are restricted to lateral margins in apical 1/3.

Female. (Fig. 6A,B); 9mm long; macropterous and known to be capable of flight; coloured as for male except for pale light organ in sternite 7, and yellow sternites 8, 9.

Pronotal outline and punctures, and form of elytra, as for male. Head form of winged female head type (Fig. 6B), not conspicuously smaller than that of male, GHW 11 × SIW; ASD > ASW; vertex shallowly excavated. Abdomen not protruding beyond elytral apices; median posterior margin of sternite 8 shallowly and broadly emarginate; sternite 9 tapering posteriorly, median posterior margin entire.

Larva. Unknown.

DISTRIBUTION. Gulf of Carpentaria islands, Northern Territory near rivers, far N Qld (Fig. 8).

REMARKS. Lea (1921b) emphasised its distinctiveness from the only other similarly coloured Australian species, *Luciola dejeani*. Both these pale species conform in colour pattern to *Lampyris incerta* Boisduval, described from New Holland. (listed here as *Species Incertae*). McDermott (1966) listed 40 Indomalaysian Luciolini with this dorsal colour pattern. The single female was taken when many other flashing specimens were observed flying (M. Schneider, pers. comm.).

Atyphella ellioti Ballantyne sp. nov.
(Figs 1, 3)

TYPE. Holotype.♂, Australia, N Qld: 19.16S, 146.49E, Mt Elliot NP, Upper North Ck, 1000m, 2-5.xii.1986, RF, GBM, GT, SH (QMT61104).

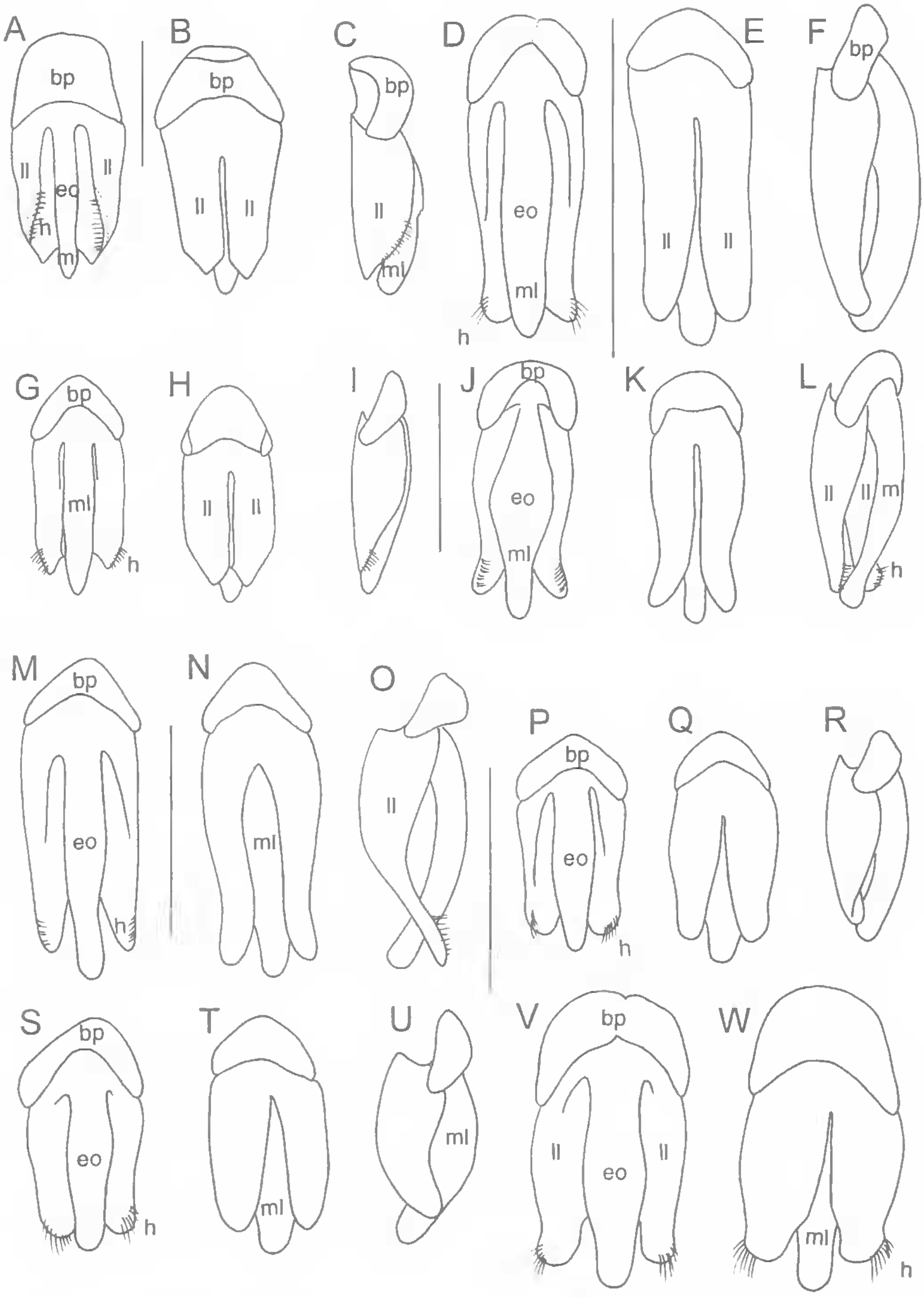

FIG. 5. Aedeagi, ♂ *Atyphella* ; A, D, G, J, M, P, S, V, ventral aspect; B, E, H, K, N, Q, T, W, dorsal aspect; C, F, I, L, O, R, U, right lateral aspect. A-C, *A. majuscula*; D-F, *A. olivieri*; G-I, *A. costata*; J-L, *A. flammans*; M-O, *A. immaculata*; P-R, *A. lychnus*; S-U, *A. similis*; V, W, *A. scintillans*. Scale lines 1mm; lines shared by: A-C & G-I; D-F & S-W; J-L; M-O; P-R. bp = basal piece; eo = ejaculatory orifice; h = hairs; ll = lateral lobe; ml = median lobe.

MATERIAL. Holotype and 11 paratypes: N QLD: same data as holotype, 4♂ (QM). 19.30S, 146.57E, Mt Elliot summit, 1150m, Jan-Mar,1991, A. Graham, PF and FIT, RF, 1♂. C QLD 21.07S, 148.31E, Pease's Lkt, Eungella, 900m, 17.xi.1992-mid April 1993, GBM & DC, RF FIT and PF, 6♂.

DIAGNOSIS. The smallest *Atyphella* species in Australia (3.6-3.9mm long); pronotum brown, elytra light brown with 2 paler interstitial lines (3, 4); mouthparts small, probably non-functional; frons-vertex junction rounded. Female and larva not associated.

DESCRIPTION. *Male*. 3.6-3.9mm long; pronotum brown, median area slightly darker than margins, pronotal punctures often ringed with brown; MS, MN and elytra light brown, except for paler suture, apex and interstitial lines (1, 2); ventral surface of thorax moderately dark brown, legs pale brown; ventral abdomen very dark brown except for white light organ in sternites 6, 7; (the dark colour of tergites 6 and 7 may be visible through the paler cuticle of sternites 6 and 7 and confuse the outline of the light organs in those segments); basal abdominal tergites light brown, tergites 5-7 very dark brown, tergite 8 pale.

Pronotum 1.1-1.2mm wide, 0.6-0.7mm long; W/L 1.8 (holotype); midanterior margin gently rounded, projecting moderately beyond rounded anterolateral corners; lateral margins slightly divergent posteriorly; disc barely depressed, lateral areas flat; punctures broad, shallow, contiguous over all of disc. Elytra with 2 well defined interstitial lines (1, 2).

Head largely concealed beneath pronotum at rest, moderate depression between eyes, GHW 0.6-0.7mm, SIW less than 0.1mm, ASD < ASW but sockets not contiguous; frons low, height subequal to ASW, and frons-vertex junction rounded; mouthpart complex small, probably non-functional; apical segment of labial palpi fusiform. Antennal length subequal to GHW, with 6-9 flagellar segments; FS 1 elongate, narrowed at base, about 3 times as long as each of the remaining subequal FS.

Abdomens of most specimens examined are shrivelled and distorted and description relates to holotype only. Light organs (Fig. 3C) occupying sternites 6 and 7 entirely, (apparently retracted to anterior 2/3 in sternite 7 in damaged paratypes); MPP of sternite 7 moderately produced, apically rounded; lateral margins of tergite 8 taper posteriorly, median posterior margin of tergite 8 rounded, and projecting a little beyond postero-lateral corners.

Aedeagus L/W 3.5; basal piece not hood like; ML not expanded at level of EO or at apex, and projecting beyond apices of lateral lobes a little and curving slightly dorsally; LL slightly expanded at their apices, widely separated along their dorsal length.

DISTRIBUTION. Far N Qld on the upper parts of Mt Elliot in rainforest, and at Eungella; never below 900 metres.

REMARKS. This small distinctive species is named from its type locality. It and *A. flammans* are the only two *Atyphella* which occur both north and south of the dry barrier between Townsville and Mackay.

Atyphella flammans Olliff
(Figs 1, 4, 5, 7, 12, 36B)

Atyphella flammans Olliff, 1890: 651. Lea, 1909: 111; 1921b: 68. Olivier, 1910: 46. Ballantyne in Calder, 1998: 176 (comb. rev.).
Luciola (Luciola) flammans (Olliff). McDermott, 1966: 104.

TYPE. Lectotype, ♂ (designated here), 20.42S, 140.30E, Cloncurry (K33979, AM). Of two ♂ on the one card bearing a holotype label, this specimen on the left has a relatively intact head (missing antennae). Chosen as lectoype as nature of frons-vertex junction is essential in distinguishing this and other similarly coloured species. Paralectotype, second ♂ on same card as lectotype, this specimen is missing its head, and has abdomen and aedeagus dissected; otherwise labelled as for lectotype (AM).

MATERIAL. Lectotype, paralectotype and 103 specimens. N QLD: 15.42S, 145.13E, Bloomfield Rd., via Helenvale, 2.x.1974, GBM, 1♂ (QM). Mt Finnigan, via Helenvale, 850-950m, 3-5.xii.1990, GBM, 1♂. 16.03S, 145.25E, Mt Halcyon, 870m, 22-24.xi.1993, GBM, 2♂. 16.05S, 145.17E, Gold Hill, McDowall Ra., 1.xi.1976, TW & R. Taylor, 2♂ (ANIC). 16.05S, 145.26E, Tribulation transect site 7, 700m, RF, 19.xi.1998, GBM, P. Bouchard, A. O'Toole, 1♂ (QM). 16.08S, 145.26E, Noah Ck, 7km ENE of Thornton Peak, 27.iii.1984, A. Calder & TW, ANIC berlesate 946, lowland RF, 1 larva (ANIC). 16.45S, 145.37E, Black Mt Rd 7km NNW of Kuranda, 30.iii.1985, 400 m, A. Calder & TW, ANIC berlesate 949, RF, 1 larva. 16.49S, 145.38E, Kuranda, F. P. Dodd, 3♂ (SAM, ANIC, MV). 6kms NW of Kuranda, 6.xi-10.xii.1984, RS & Halfpapp, 1♂ (DPI). 16.55S, 145.46E, Cairns: 3♂, (QM, ANIC). Crystal Cascades, via Cairns, 9.xii.1964, GBM, LP, 7 larvae (T.121, UQ); 12.xi.1965 GBM, 1♂ (T.180), 30.xi.1965, GBM, 1 larva (T.199); 6.xii.1966, BC, 1♂ (T.211). 17.07S, 145.41E, Upper Mulgrave R 1.xii.1965, GBM, 1♂ (T.178). Little Mulgrave R, HH, 2♂ (SAM). 17.16S, 145.53E, Bellenden Ker Ra., 1km S of Cable Tower 6, 25-31.x.1981, 500m, Earthwatch/Q Museum berlesate 321, RF sieved litter, 1 larva (ANIC). 17.17S, 145.57E, Graham Ra., 350m, 1.xi-8.xii.1995, GBM, FIT, 1♂ (QM). 17.34S 145.55E Coorumba, R. Mulder,

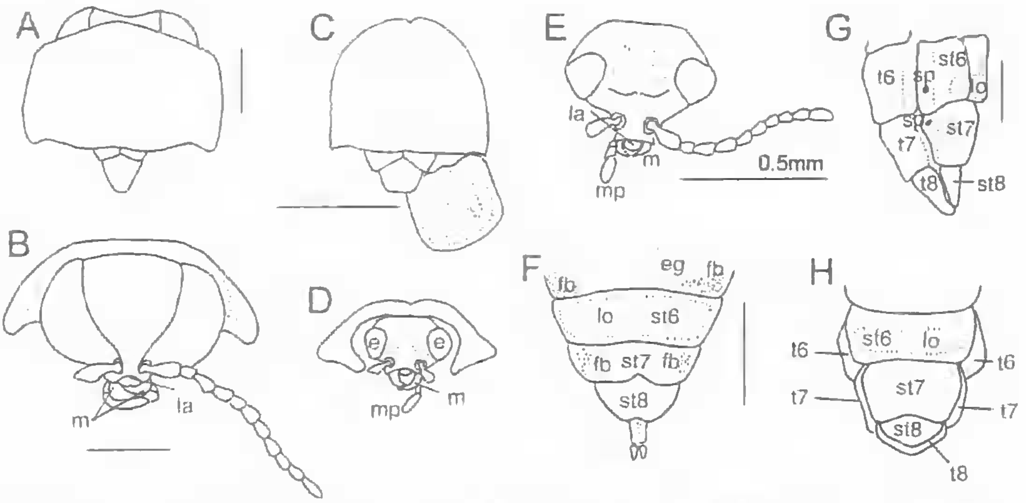

FIG. 6. ♀ *Atyphella*. A, C, dorsal aspect pronotum including head and mesonotal plates (A), and mesonotal plates and right elytron (C); B, D, E, anterior aspect head with pronotum (B, D); F-H, terminal abdomen, lateral (G) and ventral (F, H). A, B. *A. costata*; C, D, *A. inconspicua*; E, F, *A. atra*; G, H, *A. conspicua*. Scale lines 1mm; lines shared by D, F; G-H. e = eye; eg = egg; fb = fat body; la = labrum; lo = light organ; m = mandible; mp = maxillary palp; sp = spiracle; st 6-8 = sternites 6-8; t6-8 = tergites 6-8.

29-30.x.1985, 10♂; 15.xi.1985, 9♂ (AM). 17.36S, 145.45E, Henrietta Ck, 6.xii.1965, GBM. 1 larva (T.191, UQ, taken with larvae of *A. olivieri*). 17,52S, 146.07E, Clump Point, 60mi. S of Cairns, ix.1951, J. Sedlacek, 2♂ (CAS, MV); 23.x.1951, J. Campbell, 2♂ (MV). 17.53S, 146.06E, Mission Beach, 10.xi.1965, GBM, 4♂ 4 larvae (2♂ T.179 UQ, 2♂, 2 larvae T.200, 1 larva T.244; 1 larva QM); x.1951, J. Sedlacek, 1♂ (UQ). 18.39S, 146.10E, Broadwater Park, 35km NW of Ingham, 21-22.xii.1986, S.H., 2♂ (QM). 21.01S, 148.36E, 15km NE of Eungella, 18.xi.1981, A. Gillison, 950m, berlesate, meso-notophyll forest 25, 3 larvae (ANIC). 21.09S, 149.11E, Mt Blackwood, 28km NW of Mackay, 3.vii.1991, 590m, GBM, HJ, 1 larva, 1♂, 2 ♀, eggs and 7 first instar larvae (QM). 21.10S, 148.31E, Broken R, Eungella, 750m, 16-17.xi.1992, GBM, 27♂. 21.37S, 148.59E, Stony Ck, 280m, 4.x-17.xii.1999, FIT, DJC, 9♂.

DIAGNOSIS. Male often large (8-13mm long); pronotum cream with median dark markings; elytra moderately dark brown, with lateral, sutural and apical borders cream, and interstitial lines 2, 3, 4 cream where they traverse the brown area; elytra slightly convex sided when closed; antennal sockets contiguous or nearly so; mouthparts small, may be non-functional; frons-vertex junction convex. Female with fully developed elytra and abbreviated hind wings. Larva dorsally cream with patchy brown markings on tergites 2, 3 and abdominal tergite 5.

DESCRIPTION. Males are redescribed; females and larvae are newly described.

Male. 8-13mm long (lectotype 10mm); pronotum cream, with median dark markings, MS and MN cream; elytra brown with broad lateral margin, apex, sutural margin, humeral angle and interstitial lines 1-3, cream; head antennae and palpi dark brown; ventral pro and mesothorax cream, metathorax dark brown; legs 1, 2 dark brown except for pale coxae, trochanters and base of femora; ventral abdomen dark brown, almost black, except for cream sternites 6 & 7; basal tergites brown, tergites 7 & 8 pale; 7 sometimes dingier than 8 but paler than rest.

Pronotum (Fig. 1I) 2.8-4.4mm wide, 1.5-2.3mm long; W/L 1.8-2.6 (lectotype 2.0); midanterior margin sometimes slightly indented, moderately produced beyond anterolateral angles; lateral margins diverging posteriorly in anterior 3/4-5/6 with no convergence in posterior 1/6, or convergent in posterior 1/6; midposterior margin broadly indented; punctures broad, shallow, may be separated by their width in median area of disk, remainder mostly contiguous. Elytra slightly convex-sided when closed, with interstitial lines 1, 2 well developed and reaching to apical 1/8, 3 not as well elevated as 1, 2, usually effaced in front and behind and occupying about 1/4 length of elytron, 4 visible and elevated, sometimes slightly so; line 4 in lectotype is well developed; (Bloomfield Road male has line 3 almost as long as rest and line 4 well elevated).

Head almost concealed beneath pronotum at rest; deeply depressed between eyes; GHW 1.9-2.7mm; SIW 0.2-0.3mm; antennal sockets contiguous; frons scarcely defined and 1-2 × ASW (2 × ASW in lectotype); frons-vertex junction rounded; mouthpart complex small, probably non functional; apical segment of labial palpi flattened and dentate. Antennal length subequal to GHW; FS 1 almost as long as scape, FS 2,3 subequal and slightly shorter than FS 1, 4-8 subequal, about as long as broad, 9 longer than broad, and apically rounded.

Terminal abdomen on lectotype and paralectotype mutilated and this description relates to other specimens examined. Sternite 7 MPP moderately produced beyond rounded posterolateral corners and apically rounded; light organ of sternite 7 does not extend into the MPP. Tergite 8 with rounded posterior margin (Fig. 4J,K). Aedeagus L/W 3; basal piece not hood like; ML very broad around ejaculatory orifice, and narrowing just before slightly bulbous apex; LL narrowing before their apices and diverging slightly along their length, widely divergent in apical 1/6; hairs borne along apical 1/4 (Fig. 5J-L).

Female. 10mm long; fully developed elytra not covering gravid abdomen entirely and expanding slightly in posterior half; hind wings about 3/4 as long as elytra, flightless; coloured as for male, except for pale sternites 8, 9 and elytra may have light brown colouring restricted to basal 1/4 (darker hind wings visible beneath pale elytra may confuse interpretation of this dark basal area). Pronotal outline as for male. Elytra convex-sided when closed; with 4 well-defined interstitial lines, lines 2 and 3 converging in apical 1/6. Head very small, of form of wingless female head; mouthparts well developed; posterior margin of abdominal sternite 8 entire; median posterior margin of sternite 9 indented.

Larva. (Figs 12A, 36B); lateral margins of terga 1-11 bearing fine short hairs and spines, not conspicuously thickened or ridged; median line on terga 2-11 not laterally ridged; punctures in anterior half of terga 2-10 not conspicuously larger than rest. Protergum 1.1-4.0mm long; 1.8-6.5mm wide; median anterior area of protergum slightly narrowed and median anterior margin indented; lacking tubercles; posterolateral corners of thoracic and abdominal terga (except tergum 12) rounded. Posterolateral corners of terminal abdominal tergum slightly produced. Head wider than long; anterior margin laterally and medially emarginate (Fig. 7M).

Dorsally yellowish with dark brown markings; protergum with brown area along midanterior margin, lateral areas clear yellow, remainder marked lightly and patchily in brown; meso and metaterga deep cream- light brown, with small dark brown areas at anterolateral and posterolateral angles, and median area mid-dark brown; metatergum with extensive median dark brown area which widens posteriorly; abdominal terga very lightly marked in brown, except for paired small dark brown areas along midanterolateral margin of terga 4-11, and a median dark area on tergum 8; tergum 12 cream with brown markings; legs dark brown; thoracic sternal plates lightly marked with pale brown; thoracic epipleural plates dark brown; sternal plates of abdominal segments 4-10 mainly cream with light brown markings; epipleural plates of segments 4-9 dark brown with wide cream areas; epipleura of segments 9-10 cream; ventral surface of segments 10-11 pale.

DISTRIBUTION. Modern records show the species is widespread in the Wet Tropics of N Qld, ranging from just north of the Bloomfield R south to near Ingham. Farther south it has been taken at two localities near Mackay and Sarina. All these records are from tropical coastal habits, mostly in lowlands. By contrast the original types are labelled ‘Cloncurry’ which is an arid rocky region from which it has never been recollected. The Cloncurry locality requires modern confirmation and the locality is consequently omitted from distribution maps (Figs 8, 11).

REMARKS. Second largest Australian firefly. Specimens taken at Crystal Cascades near Cairns flew slowly at about head height and were easily netted.

Atyphella flammulans Ballantyne sp. nov.
(Figs 1, 4)

TYPE. Holotype.♂, N Qld 17.56S, 145.56E, Boulder Ck via Tully, 24-27.x.1983, 500-600m, GBM, DY, GT (QMT61110).

MATERIAL. Holotype and 30 paratypes. N QLD: 17.17S, 145.54E, Bellenden Ker Base Stn, 100m, 28.viii-20.x.1991, FIT, GBM and HJ, 7♂ (QM). Bellenden Ker Ra., Cable station 5, ix-x.1982, malaise trap, S. Montague, 1♂, 17.28S, 146.01E, Stone Ck, 1.x-1.xi.1995, 100m, FIT, J. Hasenpusch, 11♂. 17.36S, 146.00E, 15km WNW S Johnstone, 29.ix.1986, light trap, Faveri and Halfpapp, 1♂ (DPI). 17.47S, 145.34E, Tully Falls SF, 18km SSW of Ravenshoe, 1.x-5.xi.1987, 730m, RS & Dickinson, 2♂ (QM). Ravenshoe SF, Tully Falls Road, 10.x-15.xi.1987, RF FIT, AWH, 2♂ (OTT). 17.56S, 145.56E, Boulder Ck via Tully, 24-27.x.1983, 500-600m, GBM, DY, GT, 5♂ (QM). 17.56S, 145.56E, Upper Boulder Ck via Tully, 24-27.x.1983, 650-900m, GBM, DY, GT, 1♂.

DIAGNOSIS. Similar to *A. flammans*, differing in the smaller size (6-8.6mm long), the elytral colouration, the presence of only two well defined interstitial lines, the high frons and acutely margined frons-vertex junction.

DESCRIPTION. *Male*. 6-8.6mm long; pronotum pale clear cream with median dark brown marking (Fig. 1K); MS and MN pale cream; elytra moderately dark brown with pale cream lateral margin, apex, sutural margin, and interstitial lines 1, 2 (sometimes with traces of a short pale interstitial line 3); head dark brown, antennae and palpi mid brown; ventral surface of pro and mesothorax pale brown, of metathorax brown, darker brown in median area; legs 1 and 2 with pale semitransparent coxae, trochanters and femora, and brown tip of femora and tibiae and tarsi; legs 3 similarly coloured except for brown ventral face of coxae; abdominal sternites moderately dark brown except for pale light organ in sternites 6 and 7; abdominal tergites pale to dark brown except for paler brown tergite 8.

Pronotum (Fig. 1K) 1.4-1.6mm long; 2.4-3.0mm wide; W/L (holotype) 1.7; midanterior margin broadly rounded, projecting beyond rounded anterolateral corners; lateral margins divergent posteriorly, sometimes converging in posterior 1/4; punctures broad, shallow, contiguous. Elytra slightly convex-sided when closed, with 2 well-defined interstitial lines (1, 2) and faint traces of line 4 at base near humeral angle.

Head partially concealed beneath pronotum at rest; deeply depressed between eyes; GHW 1.5-2.0mm; SIW 0.1-0.2mm; antennal sockets contiguous; frons high, 5-6 times ASW; frons-vertex junction narrowly acute; mouthparts small; apical segment of labial palpi dentate. Antennal length subequal to or slightly > GHW; FS 1, 2 subequal in length, FS 1 narrower than 2; FS 2, 3, 4 subequal in width, 2 slightly longer than 3 which is slightly longer than 4; FS 5-9 shorter than 4, subequal in length.

Light organs (Fig. 4G) occupying anterior half or less of sternites 6 and 7 or retracted from all margins in sternite 6 (this may be a post mortem change); in sternite 7 irregular patches of fat body behind the well defined light organ material do not extend more than 2/3 median length of this sternite; MPP of sternite 7 moderately produced and apically rounded; posterior margin of tergite 8 rounded. Aedeagus like that of *A. flammans*; ML projecting strongly between apices of LL which are separated along their length dorsally with their apices divergent.

Female and Larva. Unknown.

DISTRIBUTION. Rainforest species, restricted to blocks 13 and 14 in the central part of the Wet Tropics, N Qld. It occurs from lowlands to moderately high elevation (Fig. 11).

REMARKS. The specific name *flammulans* was chosen not to represent its light pattern, which is unknown, but to emphasise its similarity to *A. flammans*.

Atyphella immaculata Ballantyne sp. nov. (Figs 4, 5)

TYPE. Holotype.♂, N Qld: 15.49S, 145.17E, Mt Finnigan, RF, 760 m, via Helensvale, 20-27. vii. 1974, GBM, DC (QMT61139).

MATERIAL. Holotype and 22 paratypes. N QLD: same locality as holotype, 8♂ (QM). 17.00S, 145.26E, 26km up Tinaroo Ck Rd, via Mareeba, 24.viii-29.ix.1983, RS & Brown, MDPI FIT, 1♂ site 8, 1♂ site 7 (DPI). 17.16S, 145.29E, Atherton, 6.x.1959, G. Ettershank, 1♂ (T.4, UQ). 17.21S, 145.36E, Malanda, 29.ix.1930, A.J. Turner, 2♂ (QM). 17.25S, 145.28E, Hugh Nelson Ra., 21km S of Atherton, 3.ix-1.xi.1984, MDPI FIT site 16, 1♂ (DPI). 17.33S, 145.32E, BS2 Mt Fisher, FIT JCU, 3.x-2.xi.1996, L. Umbach, 1♂; 1150m, malaise trap, 2♂ (ANIC). 17.37S, 145.34E, BS3 Massey Ck, 1000m, 3.x-2.xi.1995, L. Umbach, 5♂ (3 in FIT).

DIAGNOSIS. Male moderately large (7-9mm long); pronotum orange; elytra dark brown with 3 well developed interstitial lines; distinguished from *A. majuscula*, which has similar dorsal colouration, by its smaller size, parallel-sided elytra with 3 interstitial lines, and absence of a hood like basal piece of the aedeagus.

DESCRIPTION. *Male*. 7-9mm long; pronotum uniformly orange yellow; MS and MN paler orange; elytra moderately to very dark brown; head reddish brown, antennae and palpi moderately dark brown, apical segment of maxillary palpi pale on inner face; ventral surface of pro and meso thorax yellow, of metathorax mid-brown; legs yellow except for dark brown apices of femora, and all of tibiae and tarsi; ventral surface of abdomen shiny dark brown except for waxy white sternites 6 and 7; basal abdominal tergites dark brown, tergites 6, 7 and 8 pale with scattered light brown markings, tergite 6 sometimes dark brown.

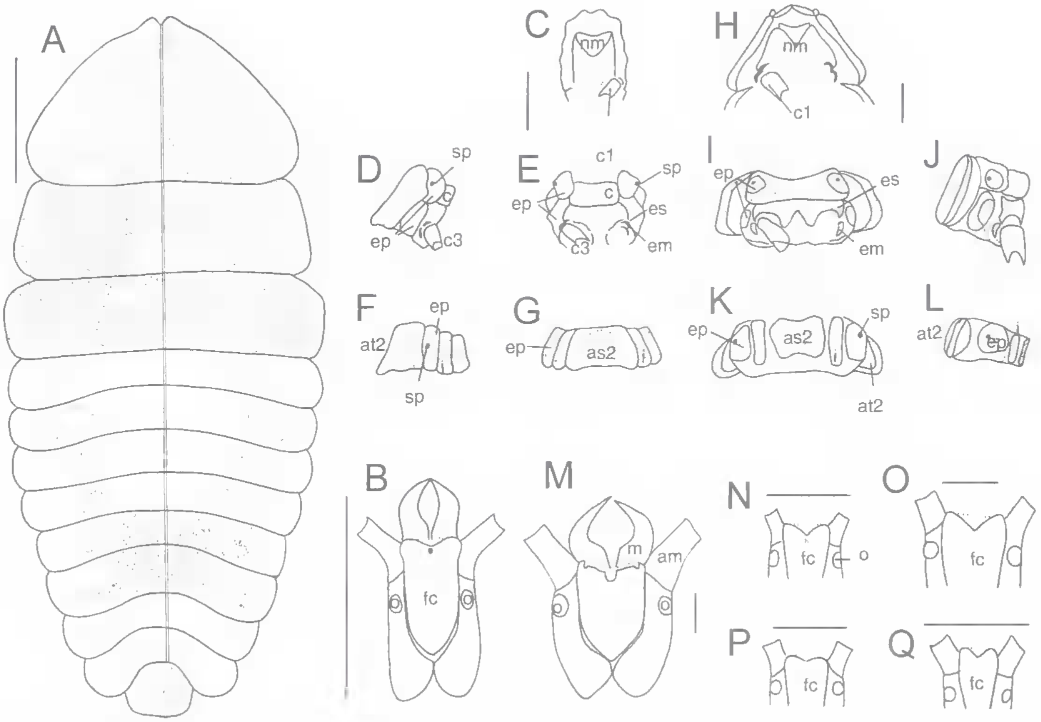

FIG. 7. Larval morphology. A, dorsal aspect; B, M, dorsal aspect larval head with base of antennal articulating membrane and mandibles; C, H,ventral aspect pronotum with head removed; D, E, J, I, lateral and ventral aspects thoracic segment 3; F, G, L, K, lateral and ventral aspects abdominal segment 2; N-Q, dorsal aspect of anterior half of larval head (semidiagrammatic). A, B, *A. atra*; C-G, *Luciola australis*; H-L, *Atyphella scintillans*; M, *A. flammans*; N, *A. olivieri*; O, *A. scintillans*; P, *A. similis*; Q, *A. lychnus*. Scale lines 1mm: lines shared by: C-G; H-L. am = antennal membrane; as2 = abdominal sternite 2; at2 = abdominal tergite 2; c = complementary segment; c1, c3 = coxae = legs 1 and 3; ep = epipleurum; es = episternum; fc = frontoclypeus; i = intrasegmental membrane; m = mandible; nm = neck membrane; o = simple eye; sp = spiracle; t3 = thoracic tergite 3.

Pronotum 2.2-3.0mm wide; 1.3-1.6mm long (W/L holotype 2); midanterior margin rounded and may project considerably beyond antero-lateral corners; punctures broad, shallow, contiguous. Elytra parallel-sided, with 3 well-defined interstitial lines (1, 2, and 4).

Head partially concealed beneath pronotum at rest; moderately depressed between eyes; GHW 2.0-3.2mm; SIW 0.2-0.3mm; ASD < ASW; antennal sockets slightly protuberant; frons 1-2 × ASW and frons-vertex junction rounded; mouthparts well developed; apical segment of labial palpi fusiform. Antennal length subequal to GHW; FS 1-4 longer than wide; FS 5-8 subequal and about as long as wide.

Light organs (Fig. 4B) occupying sternites 6 and 7 except for a narrow posterior margin of 7; MPP of sternite 7 scarcely developed and posterior margin of sternite 7 broadly rounded; lateral margins of tergite 8 subparallel and posterior margin gently rounded (Fig. 4E). Aedeagus (Fig. 5M-O) L/W 2.5; basal piece not hood-like; ML not conspicuously swollen around EO or at apex, often protuberant dorsally between apices of LL which are very narrow in lateral aspect, widely separated along their dorsal length and slightly divergent at their apices; hairs restricted to apical 1/3 or less.

Female and Larva. Unknown.

DISTRIBUTION. Restricted to the Wet Tropics of N Qld where it occurs on Mt Finnigan (block 1), and along the western edge of the central mountain system (blocks 7, 9 &10). Strictly an upland rainforest species, ranging from 750-1200m (Fig. 13).

REMARKS. The specific name, *immaculata*, meaning 'spotless' highlights its uniformly

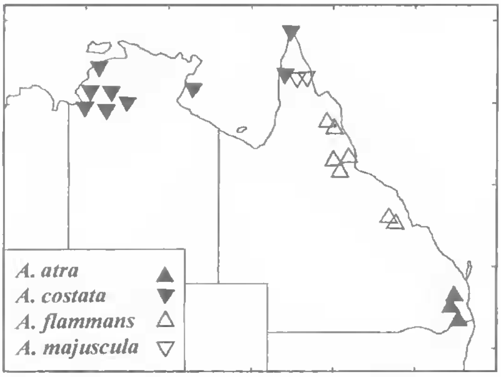

FIG. 8. Records for four Australian species of *Atyphella*.

coloured pronotum. This is one of only two Australian *Atyphella* species (the other is *A. majuscula*) which possess this dorsal colouration of orange pronotum and black elytra, a pattern associated with Australian and New Guinean *Luciola* and *Pteroptyx* (Ballantyne, 1987a,b).

Atyphella inconspicua (Lea)
(Figs 1, 2, 3, 6)

Luciola inconspicua Lea, 1921a: 197.
Luciola (Luciola) inconspicua Lea. McDermott, 1966: 106.
Atyphella inconspicua (Lea) comb. nov. Ballantyne in Calder, 1998: 177.

TYPES. Lectotype. ♂ (here designated). N Qld: 16.55S, 145.46E, Cairns district, E. Allen, male (of 2♂ mounted on card, the lectotype is mounted ventral side facing up; labels are: 1. *Luciola inconspicua* Lea Cotype Cairns; 2 C/2289; 3 Cotype) (QM). Paralectotypes, 19♂, same data as lectotype, (1 QM; 4, SAM; 4, AM; 6, MV; 2, ANIC; 2 BMNH).

MATERIAL. Lectotype, paralectotypes and 279 specimens. N QLD: no other information, 13♂ (CAS). 15.53S, 145.13E, Mt Misery Rd, 730m, 2.i.1991, ANZSES, pyrethrum knockdown, 1♂ (QM). 16.37S, 145.20E, top of Mt Lewis, 27.xi.1965, GBM, 1♂ (T.189, UQ). 16.55S, 145.25E, Mt Halcyon, 870m, 22-24.xi.1993, GBM, 2♂ (QM). 16.55S, 145.40E, Mt Williams, 900-1000m, 2-3.xii.1993, Cook, GBM and HJ, 7♂. 17.02S, 145.38E, Lambs Head, 10km W of Edmonton, GBM, GT, 12-13.xii.1988, 1200m, 23♂; 8-9.i.1990, 11♂. 17.03S, 145.41E, Upper Isley Ck, 750m, 29-30.xi.1993, DC et al., 10♂. 17.06S, 145.53 E South Bell Peak, Malbon Thompson Ra., 900m, 21-22.xi.1990, GBM, 8♂. 17.12S, 145.51E, Bellenden Ker Ra., 1km S of Cable Tower 6, 17.x-5.xi.1981, 500m, Earthwatch, QM, 28♂ (ANIC). 17.27S, 145.29E, Tower nr The Crater NP, 1230m, PF traps, 25.xi.1994-10.i.1995, GBM, 2♂ (QM). The Crater nr Herberton, xii. 1961, DKM, Lossin, 2♂ (AM). 17.31S, 145.37E. Millaa Millaa Falls, 5.xii.1965, GBM, 4♂ (T.197, UQ). 17.33S, 145.32E, Mt Fisher, 1150m, 1.xii.1994-3.i.1995, PZ, 2♂ FIT JCU East, 1♂ FIT JCU West (ANIC). 17.36S, 145.45E, Henrietta Ck, 6.xii.1965, GBM, 2♂ (T.185, UQ). 17.37S, 145.34E, BS 3 Massey Ck, 1000m, 3.x-2.xi.1995, L. Umbach, FIT JCU, 1♂ (ANIC). 17.50S, 145.56E, Tully R Xing, 10km S of Koombooloomba Dam, 4-5.i.1990, 750m, GBM, SRM, 3♂ (QM). 17.56S, 145.56E, Upper Boulder Ck, 11km NNW of Tully, 900m, 25-27.x.1983, 850 m, GBM, DY, GT, 10♂; GBM, GT, HJ, 16-19.xi.1984, 20♂, 4-5.xii.1989 at 800m, 1♂, 5-7.xii.1989, at 1000m, 12♂. Boulder Ck. via Tully, 500-600m, 24-27.x.1983, GBM, DY, GT, 35♂, 8♀. 18.12S, 145.45E, Kirrama Ra., Douglas Ck Rd, 800 m, 9-12.xii.1986, GBM, GT, SH, 65♂, 1♀ (taken with 2♂ *A. olivieri*, and 2♂, 4♀ *L. nigra*). 18.16S, 146.01E, Kirrama SF, via Cardwell, 16.xii.1966, BC, 1♂ (T.217 UQ, taken with 1♂ of *A. olivieri*). Kirrama Ra., Yuccabine Ck area, 600m, 9-12.xii.1986, GBM, GT, SH, 1♂ (QM).

DIAGNOSIS. Male small to medium (5-7.6mm long; lectotype 5.3mm); pronotum subparallel sided, cream with median dark brown markings; elytra light to moderately dark brown with 3 interstitial lines (which may be paler than rest) which are bordered by dense, large punctures; punctures appear dark brown in paler elytra; ASD subequal to or slightly smaller than ASW; mouthparts well developed; frons-vertex junction acute; head partially concealed beneath pronotum at rest. Presumed female brachelytral, differing from *A. conspicua* by the pronotal outline and nature of the pronotal punctures. Larva unknown.

DESCRIPTION. Males are redescribed; females are newly described.

Male. Small to medium; 5-7.6mm long; (lectotype 5.3mm); pronotum dull cream with median light to dark brown marking may extend across median half or greater; MS and MN cream; elytra uniformly light to medium brown; interstitial lines, and suture especially at base, may be paler than rest in which case punctures appear darker brown; head moderately dark, sometimes reddish brown, antennae and palpi paler brown; ventral pro and mesothorax pale, metathorax dark brown; legs 1, 2 cream with dark brown tarsi; legs 3 brown with cream femora; ventral abdomen dark brown except for pale cream sternites 6, 7; dorsal abdomen light brown except for pale cream tergites 7, 8.

Pronotum (Fig. 1E) 1.5-2.8mm wide; 1.0-2.4mm long; W/L 1.8 (lectotype); midanterior margin moderately projecting beyond rounded anterolateral corners; lateral margins subparallel-sided; acute posterolateral corners often project moderately beyond straight median posterior margin; punctures broad, mainly contiguous. Elytra parallel-sided when closed;

with interstitial lines 1, 2 well defined, and fainter traces of 4; elytral punctures broad, relatively shallow and conspicuous.

Head (Fig. 2C) partially concealed beneath pronotum at rest, deeply depressed between eyes; GHW 1.2-1.5mm; SIW 0.2mm; ASD usually < ASW (ASD is subequal to ASW in Upper Isley Ck males in QM, and subequal to 1/2 ASW in Lamb's Head males in QM); frons vertical, 3 × ASW high; frons-vertex junction well defined, narrowly acute; mouthparts well developed; apical segment of labial palpi fusiform. Antennal length slightly shorter than GHW; FS 1 about as long as scape, but narrower; FS 2, 3, 4 subequal; FS 5-8 subequal, slightly shorter than elongate, slender FS 9.

Light organs (Fig. 3G,H) occupying sternites 6, 7 completely except for a narrow posterior margin of 7; MPP of sternite 7 gently produced and apically rounded; posterior margin of tergite 8 rounded, lateral margins subparallel. Aedeagus L/W 1.9; with ML bulbous around EO and slightly bulbous at apex; LL convex-sided, divergent along their length dorsally and slightly bulbous at their apices.

Female. 6-9.5mm long; associated by similarity of label data only; brachelytral, and lacking hind wings (Fig. 6C,D). Pronotum pale brown with median darker brown marking, elytra paler brown with pale cream interstitial lines; head light brown, antennae very pale brown, rest of body pale cream and semitransparent.

Pronotum broadly rounded anteriorly, slightly indented in median anterior margin, anterolateral angles obliterated; lateral margins subparallel; posterolateral corners project slightly; surface scarcely depressed; punctures broad, shallow, contiguous. Elytra shorter than pronotum, with 3 well-defined interstitial lines, and contiguous in median line even when abdomen gravid. Head small, barely depressed between eyes, of wingless female head form (Fig. 6D); mouthparts well developed. Light organ in sternite 7 retracted from all margins; median posterior margins of sternites 8 and 9 not indented.

DISTRIBUTION. Common at many rainforest localities in the Wet Tropics zone, from rainforest block 1 south to block 15; usually above 500 metres (recorded up to 1330m). Old records of 'Cairns district' probably were not taken at sea level because modern collectors have not taken the species in lowlands. Taken with the similar *A. conspicua* at only 2 localities (Fig. 10).

REMARKS. Lea (1921a) commented on the superficial similarity of this species to *Luciola cowleyi*, and considered that *inconspicua* could have been assigned to either *Atyphella* or *Luciola*. There is a colour similarity only between distinctive species in 2 different genera.

Atyphella lewisi Ballantyne sp. nov.
(Fig. 4)

TYPE. Holotype. ♂ N Qld, 16.37S, 145.20E, Mt Lewis Road, via Julatten, 1000m, 11 Nov-25 Dec 1987, AWH, RF, FIT (ANIC).

MATERIAL. Holotype and 41 paratypes. N QLD: 15.42S, 145.13E, Mt Finnigan summit, via Helenvale, 28-30.xi.1985, 1100m, PF traps in RF, GBM, DC, 4♂ (QM). 15.48S, 145.17E, Mt Finnigan, 1060m, 4.xii1990 – 17.i.1991, Q. Mus, Anzses, FIT 4, 1♂. 15.43S, 145.17E, Big Tableland, NE corner, 21.xii.1990-9.i.1991, 618m, ANZSES FIT, 4♂. 16.05S,145.29E, Cape Tribulation, 22.ix-7.x.1982, GBM, 1♂; 4.5-5km W of top camp, 760-780m, GBM, 27.ix-7.x.1982, 1♂. 16.08S,145.17E, Cooper Ck, 13 mi. N Daintree R, 14.xi.1969, BC, 1♂ (UQ). 16.10S,145.23E, Thornton Peak, 11kms NE of Daintree, 900-1000 m, 30.x-1.xi.1983, GBM, DY, GT, 2♀ (QM). 16.28S,145.23E, Carbine Tbld, Mossman Bluff Camp, 30.xi.1990, 1000m, GBM, 3♂. Mossman Bluff Track, 5-10km W of Mossman, 20.xii.1989-15.i.1990, site 1 FIT ANZSES, 250m, GBM, 2♂. Devil's Thumb, 12km NW of Mossman, 1000m, 27.xii.1989, ANZSES expedition, 1♀. Windsor Tbld, 27.xii.1988-10.i.1989. site 2 FIT, E. Schmidt & ANSZES,1♂. Windsor Tbld via Mt Carbine, 26.xii.1983-24.i.1984, trap 15, RS & Halfpapp, 1♂ (DPI); 12.xi-26.xii.1983, FIT, site 14a, RS & AWH, 3♂. Windsor Tbld, 20.xii.1985-15.i.1986, FIT site 14d, RS & Brown, 2♂ 46km from main road, 2♂ 38km from main road. Windsor Tbld via Mt Carbine, i.1981, I Fanning 1♂ (QM). 16.37S,145.20E, Mt Lewis Road, via Julatten, 1000m, 11 Nov-25 Dec 1987, AWH, RF, FIT, 3♂ (ANIC). 16.37S,145.20E, Mt Lewis Road, 16km from highway, 18 Dec 1989-13 Jan 1990, 950m, FIT, GBM, GT, ANZSES site 2, 2♂ (QM). Top of Mt Lewis, 27.xi.1965, GBM, 6♂ (T. 11, 190 UQ). 5km N of Mt Lewis, via Julatten, 3.xi.1983, 1040m, pyrethrum knockdown in RF, DY and GT, 1♂ (QM).

DIAGNOSIS. Small species (4.8-5.7mm long), superficially similar to *A. brevis* and *A. ellioti*, distinguished from the former by the smaller size, presence of only 2 well defined interstitial lines, and a convex frons-vertex junction, and from the latter by the colouration of the pronotum and the terminal abdominal tergites and from all other Australian Lampyridae by the reduced area of the light organ in sternite 7. Female tentatively associated.

DESCRIPTION. *Male*. 4.8-5.7mm long; pronotum cream with median dark area sometimes occupying median half or greater (pronotum entirely dark brown in one Cape Tribulation ♂); MS and MN cream, often with darker brown median markings; elytra light to medium brown, often shiny, with pale wide lateral margin (extending to and including the pale interstitial line 4), pale interstitial lines 1, 2 and narrowly pale suture and apical margin; head dark brown, antennae and palpi paler brown; ventral thorax pale brown, legs pale brown except for darker brown tibiae and tarsi; abdominal tergites pale brown; basal abdominal sternites moderately dark brown; light organ in sternite 6 appears as a condensed yellow area in median area (Fig. 4H) with remainder being paler and more diffuse fat body material; in sternite 7 the condensed light organ material is restricted to lateral yellowish plaques separated by diffuse fat body.

Pronotum 0.8-1.0mm long, 1.7-1.8mm wide. W/L (holotype) 2.2; midanterior margin rounded, projecting moderately beyond rounded anterolateral corners; lateral margins divergent posteriorly in anterior 3/4 at least; punctures broad, shallow, mostly contiguous, punctures in median area may be separated by their width. Elytra slightly convex-sided when closed; with 2 well-defined interstitial lines (1, 2) and fainter traces of line 4, which may be effaced posteriorly.

Head partially concealed beneath pronotum at rest; deeply depressed between eyes; GHW 1.1-1.3mm; SIW 0.1mm; antennal sockets contiguous; frons not well defined, about twice ASW and sloping into frons such that the frons-vertex junction is not clearly defined; mouthparts small and adult may not feed. Antennal length subequal to GHW; FS1 narrower at base than remaining FS, and slightly longer and wider than 2; FS 2, 3 subequal in length, slightly longer than 4-9 which are subequal in length and width. Apical segment of labial palpi fusiform.

Light organ material in sternite 6 closely adpressed to underside of sternite in area indicated (Fig. 4H) remaining area of this sternite occupied by fat body; light organ material in sternite 7 appearing bipartite, with 2 condensed lateral plaque like areas united by fat body; this may be a post-mortem change; no information is available on light production to indicate the true extent of the light producing areas in sternite 7; MPP of sternite 7 broadly rounded; posterior margin of tergite 8 rounded. Aedeagus with basal piece not hood like; LL separated dorsally; ML not bulbous around EO or at apex, a little longer than lateral lobes and may project slightly dorsally through their apices.

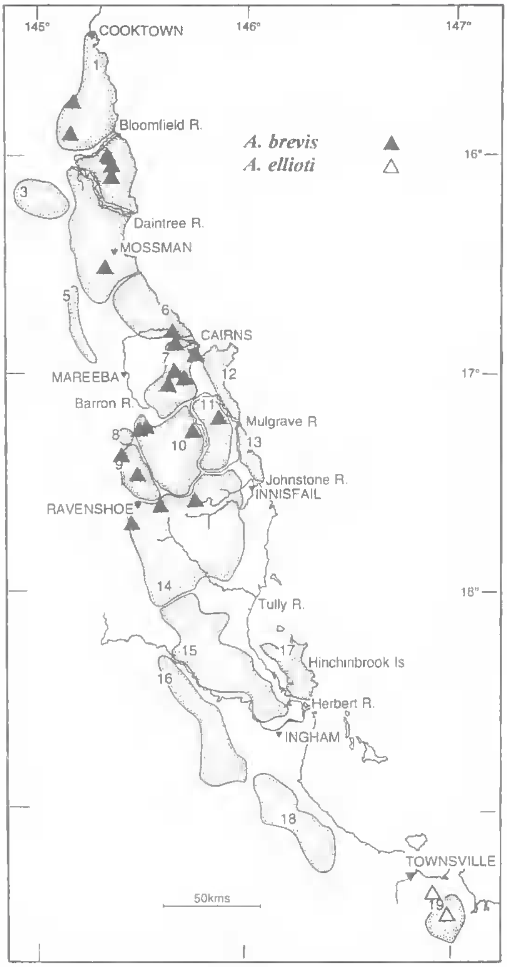

FIG. 9. Records of *Atyphella brevis* and *A. ellioti* in far north Queensland rainforests.

Female. Associated by similarity of label data only; 4-10mm long; brachelytral; elytra very short, not approaching in the median line; hind wings absent; dorsal and ventral surfaces mainly very pale yellow and semitransparent except for light brown head with very dark eyes, pale brown antennae and palpi; elytra, pronotum and MN slightly darker than rest; LO yellowish.

Pronotum broadly rounded anteriorly, not indented in anterior median line; lateral margins subparallel-sided, posterolateral corners of pronotum not projecting; dorsal surface shiny, smooth, punctures small, shallow, separated by 2-3 times their width; elytra about half as long as

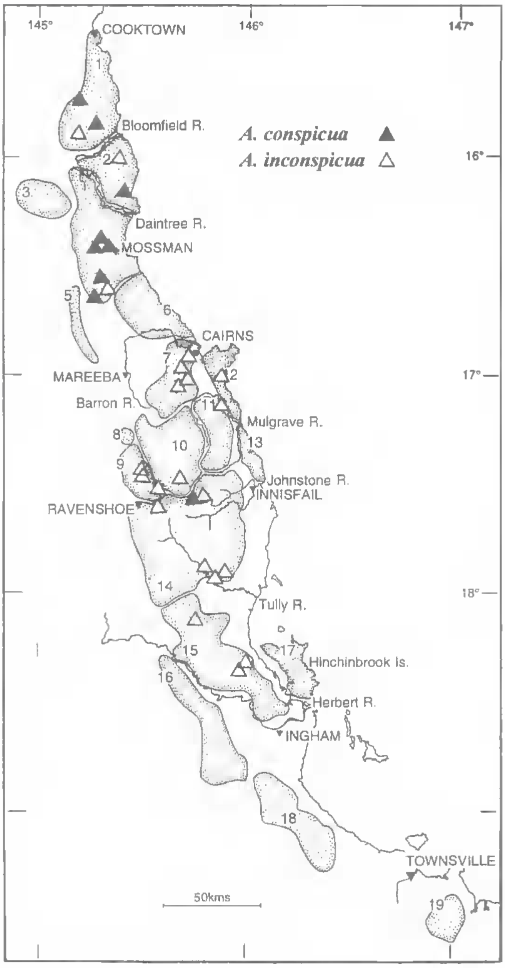

FIG. 10. Records of *Atyphella conspicua* and *A. inconspicua* in far north Queensland rainforest.

median length of pronotum, not contiguous in median line; MS very broad (about half as wide as pronotum); head small, of wingless female head form, slightly depressed between eyes; GHW = 2 × SIW; antennal length subequal to GHW; frons-vertex junction not defined. Median posterior margins of sternites 7 and 8 not indented.

DISTRIBUTION. An upland species restricted to the northern mountains (blocks 1-4) of the Wet Tropics Zone of N Qld (Fig. 13). The only record below 600m is from the Cape Tribulation coast where other upland species from adjacent mountains are also sometimes found at sea level (Monteith, 1985).

REMARKS. The species is named for its type locality.

Atyphella lychnus Olliff
(Figs 4, 5, 15)

Atyphella lychnus Olliff, 1890: 647, 1297 (female). Olivier, 1910: 47; 1911a: 172. Lea, 1909: 111; 1921c: 7. Tillyard, 1926: 213. Ballantyne in Calder, 1998: 177 (comb. rev.). *Nec* Lea, 1929: 345.
Luciola (Luciola) lychnus (Olliff). McDermott, 1966: 109. Moore, 1989: 136, Fig. 188. Lawrence & Britton, 1991: fig. 35.38, C & D (adult).
Luciola (Atyphella) lychnus (Olliff). Moore, 1989: 136.

TYPES. Lectotype. ♂ (designated here). Australia, NSW: 33.30S, 150.23E, Mt Wilson, Blue Mts, i.'89, Olliff; the left specimen of two syntypes mounted ventral side down on card, this specimen has head and abdomen dissected and mounted separately on the card (K33996, AM). Paralectotypes: 2♂, 2♀, larva, same label as lectotype (2♂, ♀, larva AM; ♂ and ♀ SAM).

MATERIAL. Lectotype, 5 paralectotypes and 114 specimens. SE QLD: 26.36S, 152.44E, Kenilworth SF, via Kenilworth, 20.x.1972, BC, 2♂ (UQ). 26.73S, 152.71E, Conondale, sites 12-13, 29.xi.1974, GBM, 2♂. NSW: 30.20S, 152.43E, Dorrigo, 1♂ (ANIC). 30.23S, 152.43E, Never Never Picnic area, Dorrigo NP, 29.xii.1989, A. Sundholm, 1♂ (AM). 30.43S, 152.55E, 12mi. S of Macksville, 11.xii.1967, T. Houston, 3♂ (QM, UQ). 31.58S, 151.55E, Barrington R., 4500ft., xii.1962, N.E.U. Exp. Soc., 2♂ (ANIC). 32.25S, 152.12E, Bulahdelah, 14.i.1932, Fuller, 3♂. 32.16S, 151.30E, Upper Allyn nr Eccleston, 16.xi.1965, DKM, 1♂ (AM); Upper Allyn, 26.i.1975, 9♂ 1♀. 32.34S, 151.10E, 'Tuglo', 48km N of Singleton, C. Smithers, 2♂ 6.xii.1977, 1♂ 3.xii.1977, 1♀ 27.i.1981, 1 larva 5.iv.1981, 3♂ 9.xii.1981, 1♀ 2.i.1983, 1♀ 2.ii.1983. 32.48S, 150.15E, (Mt.) Never Never, 30.xi. 1911, R. J. Tillyard, 1♂ (QM). 33.29S, 150.28E, Mt Irvine, i.1905, J. A., 2♂ (AM); 25.xii.1934, N. Plomley, 8♂ (BMNH); Smart, 1942, 3♂, 1♀ ; 29.i.1944, Mrs Messmer, 1♀ (AM). 33.30S, 150.23E, Mt Wilson, H.J. Carter, 6♂ (UQ), 7♂ i.1920 (ANIC), 1♂ i.1924; 1♂ i.1905 (MV); 6♂ 25.xii.1934 N. Plomley (BMNH). 33.42S, 150.23E, Blue Mtns, 2♂ (SAM); L. Sinclair, 3♂ (UQ), 3♂ (QM), 3♂ (ANIC), 8♂, 1♀ (MM), Grose Vale, Taylor, 2♂ (BMNH). 33.49S, 150.02E, Vicinity Jenolan Caves, 2♂ (BMNH); 1♂ (MV); J. Wilburd, 2♂, 2♀ (SAM); 2♂. 31.47S, 152.32E, 4km W of Lansdowne, Lorien, 5-6.xii.1986, H. & A. Howden, 1♂ (ANIC). 34.07S, 150.13E, Lannigan's Ck, Colong dist., nr Yerranderie, 10.xi.1927, A. Musgrave, T. Campbell, 2♂ (AM). 33.52S, 150.35E, nr Norton's Basin Nepean R, 10.xi.1921 A. Musgrave, 2♂, 1♀. 34.38S, 150.43E, Minnamurra Falls, 10mi. W of Kiama, H. & A. Howden, 2♂ 23.xii.1974, 1♂ 25.xii.1974 (OTT). 34.24S, 151.51E, Mt Keira, 20.ii.1967, GBM, 2 larvae (T.212 UQ).

DIAGNOSIS. Males 6.0-9.5mm long; pronotum cream with median dark markings; elytra light brown with paler lateral margin and 4 well defined interstitial lines which may be paler than rest of elytron. Female with fully developed

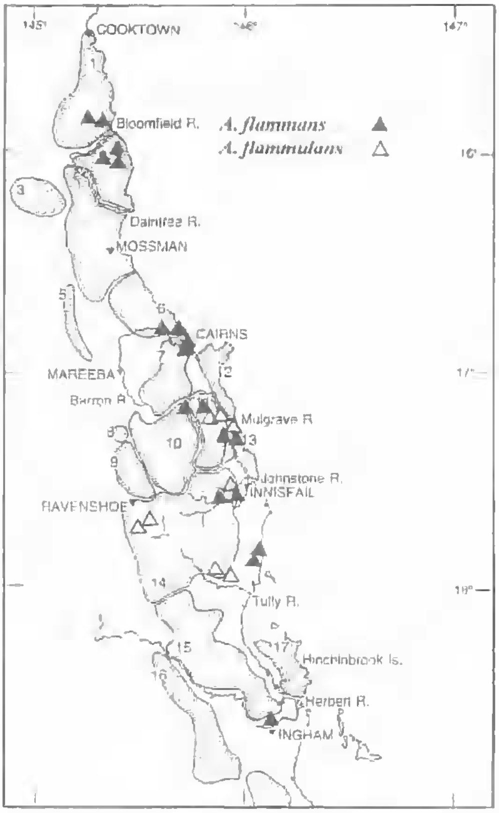

FIG. 11. Records of *Atyphella flammans* and *A. flammulans* in far north Queensland rainforest.

elytra and shortened hind wings, dorsally dingy cream. Larva dorsally cream with very extensive dark markings; similar to *A. scintillans* but lacking pronotal tubercles.

DESCRIPTION. Males, females and larvae are redescribed.

Male. 6.0-9.5mm long; pronotum dingy cream with median brown markings occupying median half or less; MS and MN dingy cream; elytra light-medium brown with interstitial lines and margins slightly paler (elytral colour of Dorrigo and Macksville males is moderately dark brown with pale interstitial lines and margins, similar to *A. flammans*; head and antennae red brown; ventral pro and mesothorax pale, metathorax dark brown; legs pale except for dingy brown tibiae and dark brown tarsi; ventral abdomen dark brown except for pale cream sternites 6, 7; dorsal abdomen very dark brown - black except for pale tergite 8 and sometimes pale posterior margin of tergite 7.

Pronotum 2.2-2.6mm wide; 1.2-1.4mm long; W/L 2.0 (lectotype); midanterior margin often pointed, lateral margins divergent posteriorly; anterolateral and lateral margins often somewhat reflexed; punctures broad, shallow, broader in lateral areas, all contiguous. Elytra parallel-sided when closed, with 4 well-defined interstitial lines.

Head covered by pronotum at rest; moderately depressed between eyes, GHW 1.2 -1.4mm; SIW 0.2mm; ASD < ASW; frons scarce, 1 × ASW, frons-vertex junction rounded; mouthparts very small, non-functional; apical segment of labial palpi fusiform. Antennal length subequal to GHW; with FS 1 slightly longer than scape, FS 2-9 shorter than FS1 and subequal.

Light organs occupying sternites 6, 7 entirely, or posterior margin of 7 very narrowly clear; MPP of sternite 7 gently produced and apically rounded; tergite 8 with lateral margins converging slightly posteriorly, median posterior margin rounded and projecting a little beyond the rounded posterolateral corners. Aedeagus (Fig. 5P-R) L/W 2.0; basal piece not hood like; ML scarcely wider at level of EO than at apex; LL divergent along their length dorsally; apices slightly bulbous but not divergent when viewed from below; hairs restricted to apical 1/3 or less.

Female. 5.7-7.2mm long; with fully developed elytra and hind wings about 2/3 as long as elytra (abdomen may protrude beyond elytral apices). Dorsal body dingy cream; pronotum with median irregular brown marking; head brown, antennae dingy cream; ventral thorax and abdomen cream.

Pronotal outline similar to that of male, anterior and posterior margins sometimes indented in the midline; punctures contiguous. Elytra fully developed, slightly convex-sided when closed; with 4 well defined interstitial lines, and either covering abdomen completely at rest or at most with 2 segments protruding. Head very small, form of wingless female; very slightly excavated between the widely separated eyes; mouthpart complex small but could be functional. Abdomen with median posterior margin of sternites 7 and 8 shallowly indented.

Larva. (Fig. 15B). Lateral margins of terga 1-10 slightly ridged, finely hairy and densely spinose; median line from anterior margin of tergum 1 to posterior margin of tergum 11 slightly elevated and bordered with hairs and small spines; punctures in anterior half of terga 2-10 not any larger than rest. Protergum 1.5-1.9mm long, 2.2-2.7mm wide; anterior margin in median and anterolateral areas indented; tubercles lacking;

posterolateral corners of protergum and terga 2-11, rounded. Posterolateral corners of tergum 12 projecting slightly. Head 1.2-1.5mm long, 1.2-1.7mm wide; broadly excavated along anterior margin (Fig 7Q).

Dorsally yellowish with dark brown markings; protergum cream with narrow dark brown margin and dark areas in posterior half; meso and metaterga very dark brown, with paired paler areas at antero- and posterolateral angles, and along posterior margin to either side of midline, or median area of tergum 3 and abdominal terga 4-9 with broad paler areas; lateral pale areas on terga 4-9 may almost coalesce, and median cream areas on at least terga 4, 5 may extend from anterior to posterior margins; terga 10, 11 largely cream, with narrow dark brown markings to either side of midline; if terga 10, 11 are mainly cream then tergum 12 is also pale; if terga 10, 11 have extensive light brown markings then tergum 12 is similarly marked; dorsum of head mostly dark brown with irregular pale areas behind ocelli; legs, and all ventral thoracic plates, dark brown; abdominal segments 4-9 with dark brown sterna with a narrow median pale strip, and brown epipleural plates with median pale markings; ventral segments 10-12 pale cream except for dark brown anterior margins of epipleural plates of segment 10.

DISTRIBUTION. Apart from two S Qld records from the Conondale Ra., this species is restricted to northeast and central NSW where some records are from rainforest (Fig. 14).

REMARKS. This species has the most southern distribution of any Australian firefly and is popularly known as the ‘Blue Mountains firefly’. Olliff (1890) described a light display at Mount Wilson. Lea (1929) recorded 6 males of *A. lychnus* from Mount Tamborine, Qld. The four males relocated at QM are *Atyphella similis* described here as new. A lectotype is designated to resolve this confusion. Figures of the ventral surface of the male in Lawrence & Britton (1991: fig. 35.38D, reproduced in Calder [1998: 172]) show two small unlabelled projections beyond the posterior margin of abdominal sternite 7; they are probably the aedeagal sheath and the tip of the aedeagus.

Atyphella majuscula (Lea)
(Figs 3, 5, 12)

Luciola majuscula Lea, 1915: 495.
Luciola (Luciola) majuscula Lea. McDermott, 1966: 109.
Atyphella majuscula (Lea) comb. nov. Ballantyne in Calder, 1998: 177.

TYPE. Lectotype.♂ (dissected) N Qld: Cape York Pen., 13.57S, 143.12E, Coen Dist., HH, 12727 (SAM). Calder (1998) regarded this single♂ as the only syntype remaining of the original material.

MATERIAL. Syntype ♂ and 78 specimens. N QLD: 12.44S, 143.14E, 3km ENE of Mt Tozer, 1-4.vii.1986, TW. ANIC berlesate 1052, RF litter, 2 larvae (ANIC). 12.44S, 143.17E, Iron Ra., 3.i.1972, PZ, 3♂ (ANIC, AM); 6.v.1968, GBM 7 larvae (UQ). 12.44S, 143.15E, W Claudie R, 4km SW of road junction, 6.xii.1986, G. Daniels, M. Schneider, 2♂ (UQ). Claudie R nr Iron Ra., 19-25.vii.1978, JL, berlesate 648, 1 larva (ANIC). Claudie R nr Mt Lamond, 8♂, 1♀, 1-5.i.1972, DKM & Holloway (AM). Iron Ra., S slope of Mt Lamond, 13.vi.1971, R. Taylor & J. Freeman, ANIC berlesate 314, RF, 2 larvae (ANIC). 13.49S, 143.28E, Rocky R, Silver Plains, E coast: 6.i.1960, JLW, 5♂ (ANIC), 5♂, 1♀ (2♂, 1♀T. 22, 25 UQ); 14.xii.1964, JLW, GBM, LP, 11♂, 1♀, (4♂, 1♀, T.117); 15.xii.1964, JLW, GBM, LP, 15♂, 1 larva (3♂, 1 larva T. 116, 119; 2♂ QM); 16.xii.1964, JLW, GBM, LP, 8♂, 1♀(1♂, 1♀ T.118 UQ). 13.52S, 142.51E, Coen R, W. Dodd, 1♀(SAM).

DIAGNOSIS. Males large (10.7-13.4mm long); pronotum orange, lacking any darker markings, elytra dark brown, with 3 well defined interstitial lines; elytra slightly convex sided when closed; antennal sockets not contiguous; mouthparts well developed; frons-vertex junction not defined. Females macropterous, coloured as for male.

DESCRIPTION. Males are redescribed; females and larvae are newly described.

Male. 10.7-13.4mm long; pronotum, MS and MN light orange; elytra dark brown; head and antennae dark brown; ventral thorax orange; legs orange except for dark brown apical 1/2 of femora and dark brown tibiae and tarsi; ventral abdomen dark brown except for pale cream sternites 6, 7; dorsal abdomen dark brown except for pale tergites 7, 8.

Pronotum 3.4-5.8mm wide; 2.0-2.7mm long; W/L 1.7; midanterior margin rounded, little if at all produced beyond rounded anterolateral corners; lateral margins diverge posteriorly in anterior half then may converge slightly; pronotal punctures broad, shallow, contiguous. Elytra slightly convex-sided when closed, with interstitial lines 1, 2, 3, well defined, and 4 ill defined.

Head not completely covered by pronotum at rest, moderately depressed between eyes; GHW 2.2-2.9mm; SIW 0.3-0.5mm; ASD subequal to ASW; frons not clearly delimited or separate from vertex, frons-vertex junction not defined; mouthparts well developed; apical segment of labial palpi flattened and dentate. Antennal length > GHW but < 2 × GHW; FS subequal in

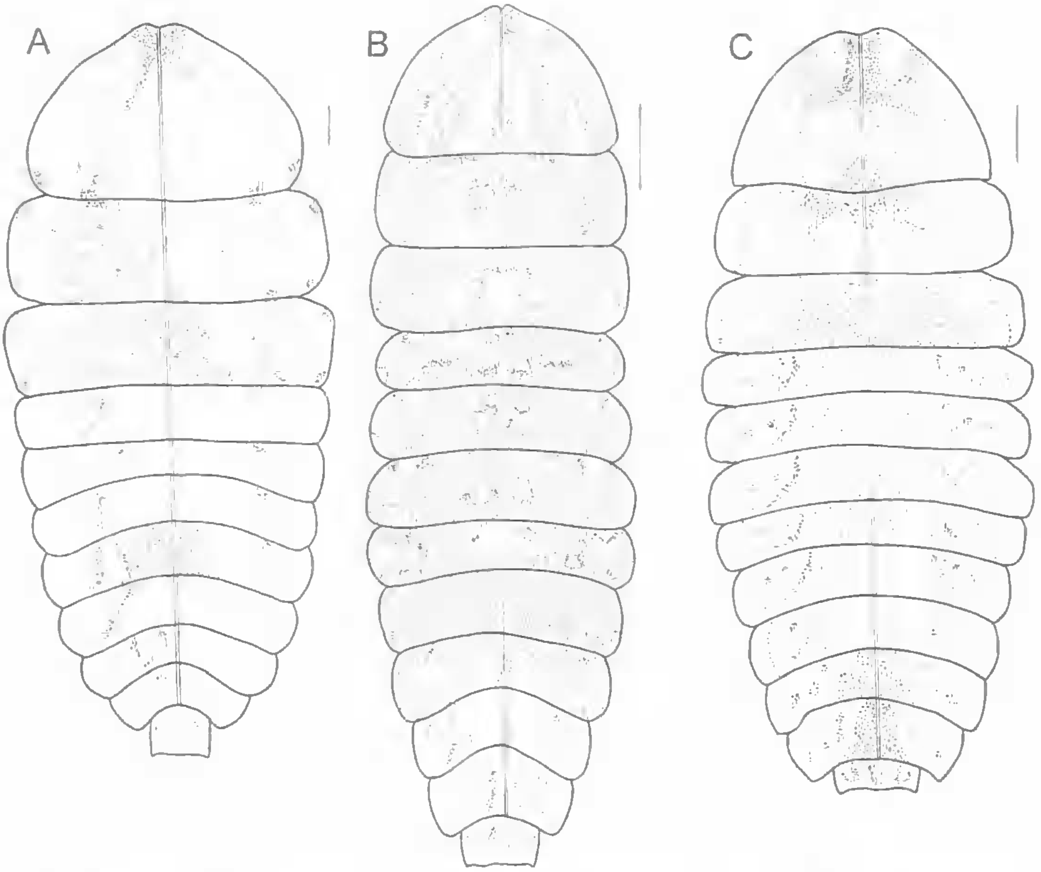

FIG. 12. *Atyphella* larvae, dorsal aspects. A, *A. flammans* (left and right sides represent different colour patterns); B, *A. similis*; C, *A. majuscula*. Scale lines 1mm.

length, longer than wide and slightly shorter than scape.

Light organs (Fig. 3J) occupying sternites 6, 7 except for narrow posterior margin of 7; MPP of sternite 7 moderately produced and apically rounded; tergite 7 (Fig. 3K,L) with lateral margins converging posteriorly; tergite 8 much narrower than 7, lateral margins converging strongly posteriorly, and median posterior margin straight; ventral surface of tergite 8 with 2 slightly sclerotised lateral longitudinal lines. Aedeagus (Fig. 5A-C) L/W 3.5; basal piece large, with anterior margin projecting conspicuously dorsally and appearing hood-like in lateral aspect; ML elongate, slender, not expanded at EO or at apex; LL approximate dorsally, very broad in lateral aspect, diverging only at their apices which are narrow; hairs borne preapically along slightly less than 1/3 of length of LL.

Female. 12mm long. Macropterous and capable of flight. Coloured as for male, except for pale light organ in sternite 7, and yellow sternites 8, 9 and tergites 7, 8.

Pronotal outline like that of male except mid-anterior margin not produced much beyond anterolateral angles; punctures as for male. Elytra with 3 well defined interstitial lines (1, 2, 3). Head concealed beneath pronotum at rest; barely excavated between the eyes, form of winged female head; GHW 5 × SIW; apical segment of labial palpi flattened and dentate. Light organ (appearing as compact fat body material) restricted to sternite 7 but sternite 8 may have irregularly distributed fat body material; median posterior margins of 8 and 9 indented.

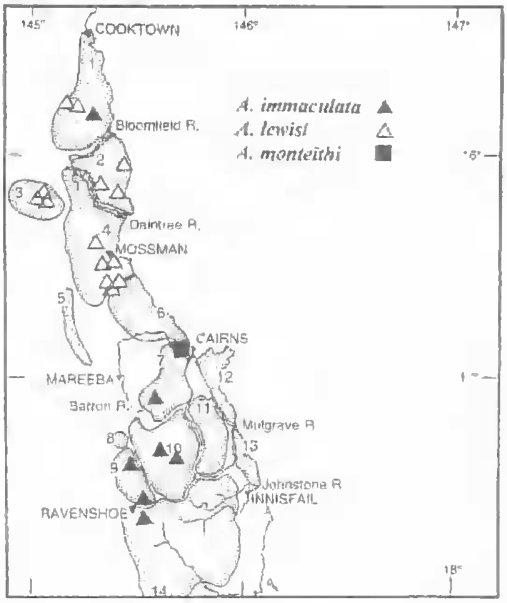

FIG. 13. Records for three species of *Atyphella* in far north Queensland rainforest.

Larva. (Fig. 12C). Lateral margins of terga 1-11 slightly ridged, hairy and spinose; median line from anterior margin of tergum 1 to posterior margin of tergum 11 not elevated or laterally margined; punctures in anterior half of terga 2-11 slightly larger than rest. Protergum 1.3-2.7mm long, 2.2-5mm wide; median anterior margin broadly and shallowly indented; protergum not narrowed in anterior 1/6; lacking tubercles; posterolateral margins of protergum and terga 2-10 acute. Posterolateral corners of terminal abdominal tergum slightly produced. Head about as long as wide; anterior margin emarginate as described for *A. flammans*. Dorsally cream, marked patchily in dark brown; protergum with an anteromedial dark brown area, otherwise patchily dark marked; mesotergum with small dark anterolateral areas; metatergum with lateral oblique dark brown strips, and median area dark brown; abdominal terga 4-11 patchily brown, (tergum 8 darker than rest); tergum 11 with wide pale lateral areas; legs pale brown; ventral thoracic plates faintly marked with light brown; abdominal segments 4-9 with dark epipleural plates (pale around spiracles); sterna of segments 4-9 pale with light brown markings; ventral surface of segments 11, 12 pale.

DISTRIBUTION. Restricted to rainforest in the Iron Ra. and McIlwraith Ra. in central Cape York Peninsula; also recorded from Papua New Guinea (Ballantyne, 1992) (Fig. 8).

REMARKS. Lea (1915) highlighted the large size of this species (it is the largest Australian lampyrid), and the pronotal shape. Ballantyne (1992) recorded it from New Guinea and distinguished the following similarly sized and coloured species: *majuscula* Lea, *guerini* Ballantyne and *salomonis* Olivier.

Atyphella monteithi Ballantyne sp. nov (Figs 1, 2, 4)

TYPE. Holotype, ♂, N Qld: 16.51S, 145.43E, Crystal Cascades, via Cairns, 9.xii.1964, GBM (QMT62709).

MATERIAL. Holotype and 2♂ paratypes collected with holotype (UQ).

DIAGNOSIS. Medium size (7.0-8.5mm long); pronotum orange with median dark marking; elytra dark brown with 3 well defined interstitial lines; elytra slightly convex sided when closed; antennal sockets not contiguous; frons-vertex junction rounded. Female and larva not associated.

DESCRIPTION. *Male*. 7-8.5mm long; pronotum dingy orange with median dark brown marking; pronotal punctures margined with deeper orange; MS and MN pale cream; elytra dark brown, suture pale brown in anterior3/4; head and antennae dark brown; labrum pale; ventral surface of pro and mesothorax light brown, of metathorax dark brown; legs 1, 2 pale except for dark brown tibiae and tarsi; legs 3 pale except for dark brown coxae; basal abdominal sternites dark brown, sternites 6, 7 pale cream; dorsal abdomen dark brown except for pale tergite 8.

Pronotum (Fig. 1I) 2.5-3.0mm wide; 1.4-1.6mm long; W/L (holotype) 1.8; midanterior margin gently rounded, scarcely produced beyond anterolateral angles; lateral margins divergent posteriorly in anterior 2/3 and slightly convergent in posterior 1/3 in holotype and one paratype, divergent along almost their entire length in second paratype; punctures broad, shallow, contiguous over all of disc. Elytra with three well defined interstitial lines (1, 2, 4) present; slightly convex-sided when closed; elytral punctures densely clustered along interstitial lines.

Head (Fig. 2A,B) small, concealed beneath pronotum at rest, moderately depressed between eyes; GHW 1.3-1.5mm; SIW 0.15-0.2mm; ASD < ASW; frons high and flat, 2 × ASW; frons-vertex junction rounded; mouthparts well developed; apical segment of labial palpi fusiform. Antennal length subequal to GHW; with FS 1 narrowed basally, about 1.5 × FS 2; FS 5-8 subequal, about as wide as long; FS 9 elongate, slender, 2 × FS 8.

Light organs (Fig. 4C,F) occupying sternites 6 and 7 except for narrow posterior margin of 7; MPP of sternite 7 moderately produced, and bluntly rounded at apex; tergite 8 with lateral margins subparallel and posterior margin rounded. Aedeagus L/W 2.2; basal piece not hood like; ML slightly expanded at level of EO but not expanded at apex; LL moderately divergent along their length dorsally and slightly bulbous at their apices; hairs along apical 1/3 or less.

DISTRIBUTION. Known only from these three specimens netted while flying and flashing at night in rainforest near Cairns (Fig. 13).

REMARKS. This rare species is named for Geoff Monteith of the QM in grateful appreciation of his continued interest and support in the collection of specimens of fireflies.

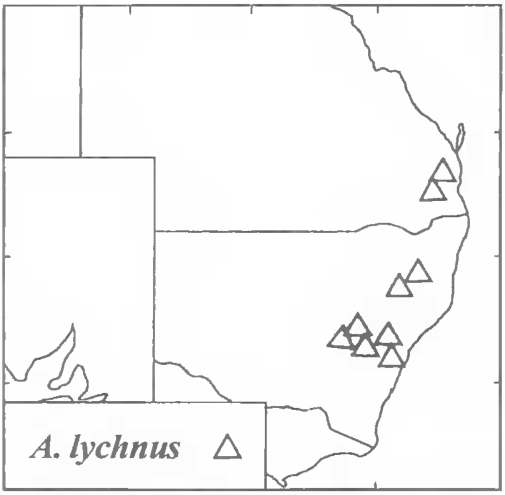

FIG. 14. Records of *Atyphella lychnus* in southeast Australia.

Atyphella olivieri Lea
(Figs 1, 2, 3, 5, 15, 36A)

Atyphella olivieri Lea, 1915: 494; 1921a: 197; 1921c: 7. Ballantyne in Calder, 1998: 177 (comb. rev.).

Atyphella Olivieri Lea. Olivier 1910: 47; 1911a: 172.

Luciola (Luciola) oliveris (Lea). McDermott, 1964: 16. Unn. nom. nov.

Luciola (Luciola) olivierius (Lea). McDermott, 1966: 110. Unnecessary name change or probable misspelling for *L. oliveris* McDermott 1964.

TYPE. Lectotype. ♂ (designated here). N Qld: 16.55S, 145.46E, Cairns (QM). The lectotype is the upper specimen of 2 syntypes mounted on card and labelled 1. C/2253; 2. COTYPE; 3. hand-written label '*Atyphella olivieri* Lea Queensland'; 'cotype' in red ink. Paralectotypes, same locality as lectotype, 34 'syntype' ♂ (AM, 6; ANIC, 6; UQ 2; SAM 8; MV, 8; QM, 2; BMNH, 2).

MATERIAL. Lectotype, paralectotypes and 267 specimens. Larval specimens # have a small dorsal elevation in the median area of pronotum 1/4 length behind the anterior margin. N Qld: 15.42S, 145.13E, Mt Finnigan summit, via Helenvale, 28-30.xi.1985, 1100m, GBM, DC, Roberts, 1♂ (QM). 15.43S, 145.17E, Big Tableland, ANZSES exp., 19-20.xii.1990 1♂. 15.48S, 145.15E, Shipton's Flat, 35km S of Cooktown, 22.iv.1982, GBM, DY, GT, 1♂. 15.50S, 145.19E, 2km NE of Mt McMillan, 500-800m, ANZSES exp., 11-13.i.1991, 2♂. 16.05S, 145.29E, Cape Tribulation, 22 ix-7.x.1982, GBM, DY, GT, 2♂. 16.03 S to 16.05S, 145.28E, Cape Tribulation area, 21-28.iii.1984, A. Calder, TW, 5♂; berlesate 939 lowland RF, 5 larvae (ANIC); 14.vii.1982, S. & J. Peck, RF leaf litter, 1 larva #. 16.12S, 145.26E, Alexandra Bay, 24.vi.1971, R. Taylor, < 50 m, ANIC berlesate 331, RF, 1 larva. 16.14S, 145.26E, Thornton Ra., 23.vi.1971, 100m, R. Taylor, ANIC berlesate 325, RF, 1 larva #. 16.28S, 145.19E, Rex Ck 5km W of Mossman, 21.iv.1997, RF night collection, C.B. & C. Pavey, 1♂ (QM). 16.28S, 145.23E, 3mi. W of Mossman, IC & MU, 25♂ 14.iii.1964, 18♂ 17.iv.1964 (ANIC). Mossman Gorge, in RF, at light, 29.x.1966, EB, 1♂. 16.37S, 145.20E, Rifle Ck, at Black Mt., 18km ESE of Julatten, 13-14. iv. 1982, in RF, 400 m, GBM, DY, DC, 1♂ (QM). 16.49S, 145.38E, Kuranda, 1♂ (CAS); 3♂ (2♂ iv.1905), F. Dodd (SAM; one♂ bears label 'descd as var of *flammans*'); 8.iii.1966, D. Havenstein, 1♂ (ANIC); 1 mi. E of Kuranda, 19.iv.1964, IC, MU, 3♂. Nr Barron Falls, Kuranda, Stop A34, 15.iii.1988, D. Rentz, 1♂. 16.55S, 145.40E, Mt Williams summit, 1000m, 27-28.xi.1997, GBM, DC, 3♂; 27.xi.1997-6.ii.1998, RF FIT, 1♂ (QM). 16.55S, 145.46E, Cairns, 26.ii.1939, GB, 6♂ (ANIC); Cairns district, F. Dodd, 1♂ (SAM); J. Anderson, 2♂ (QM). Crystal Cascades, via Cairns, 9.xii.1964, GBM, 3♂ (T.123 UQ). Boar Pocket Road, c. 8km N of Gillies Hwy, 21.ii.1970 at light, GB, 2♂ (ANIC). 17.02S, 145.38E, Lamb's Head, 10km W of Edmonton, 12-13.xii.1988, 1200m, GBM, GT, 1♂ (QM); 8-9.i.1990, 1200m, GBM, SRM, 1♀. 17.02S, 145.37E, Davies Ck (15 road km from Kennedy Hwy), 21km E by S of Mareeba, 1.iii.1988, D. Rentz, stop A28, 13♂ (ANIC). 17.06S, 145.36E, Kauri Ck, Lamb Ra., RF, 1190m, 27.xi.1998, GBM, P. Bouchard, A. O'Toole, 1♂ (QM). 17.06S, 145.37E, Mt Haig Rd, 11km NE of Tinaroo Dam, Atherton Tbld, Stop A15, 5.ii.1988, D. Rentz, 1♂ (ANIC). 17.07S, 145.41E, Little Mulgrave R, HH, 1♂ (QM), 2♂ (SAM), 6♂ (CAS). 17.15S, 145.38E, Lake Barrine, Atherton Tbld, 29.i.1988, Stop A-8, D. Rentz, 2♂ (ANIC). 17.16S, 145.29E, 4mi. S of Atherton, 16.ii.1975, H. & A. Howden, 1♂. 3.2km N of Atherton, 5.v.1970, ANIC berlesate 275, RF, 2 larvae. Ringrose NP, via Atherton, 9.xii.1966, BC, 2♂, taken with *A. brevis* (UQ). Mt Edith, 18 mi. NE of Atherton, 3400 ft., 18.iii.1964, IC, MU, 1♂ (ANIC). Tolga Scrub, nr Atherton, 28.xi.1964, R. Elder, 5♂ (UQ). 17.17S,145.34E, Curtain Fig, 2km SSW of Yungaburra, Atherton Tbld, Stop A2, ii.1988, D. Rentz, 1♂ (ANIC). 17.17S,145.58E, Graham Ra., 550m, 8-9.xii.1995, GBM, 14♂, 1♀ (QM). 17.17S,145.34E, Curtain Fig, 2km SSW of Yungaburra, Atherton Tbld, 2.ii.1988, Stop A-2, D. Rentz, 1♂ (ANIC). 17.21S,145.46E, Tolga, 5.i.1984, R. Lachlan, 4♂ (AM). 17.23S,145.23E The Crater nr Herberton, xii.1961, DKM, 12♂, 1♀. 17.31S,145.37E, Millaa Millaa Falls, via Millaa Millaa, GBM, 9.i.1964, 1♂ taken with *A brevis* (T.26 UQ), 5.xii.1965, 10♂ (T.196); 10-11.xii.1966, BC, 13♂; 16.iv.1997, GBM, Russell, Ovenden, 1♂ (QM). 17.32S,146.01E, Innisfail, J. Gilchrist, xii.1963, 6♂ (T.5 UQ), 1♂ i.1964 (T.28); 4♂ (ANIC); 3♂ (MV). 17.33S,145.31E. Chilverton, 22.xii.1964, H. Rose, 1♀ (T.124 UQ). 17.36S,145.45E, Henrietta Ck, Palmerston NP, GBM, 6.xii.1965, 2♂, 1 larva (2♂ T.184, 1 larva T.195 UQ), 23.iv.1970, 3♂, 29.xii.1964, 9♂ (T.129), 12.xii.1966, BC, 3♂. 17.46S,145.35E, Cardstone, via Tully Falls, 10.v.1983, 200m, GBM, DY, 1♂ (QM). 17.50S,145.36E, Tully R crossing, 10km S of Koombooloomba dam, 4-5.i.1990, 750m, GBM, SRM, 3♂. Cardwell Ra., Mt Macalister, 800-900m, 13-16.i.1987, SH, 4♂. Kirrama Ra., Douglas Ck Rd, 800m, 9-12.xii.1986, GBM, GT, SH, 8♂. 17.54S,145.41E, Mt Kooroomool summit, 7km S. 1050m, RF, 3-4.xii.1998, GBM, DC, P Bouchard, 2♂. 18.59S,146.09E, Star Valley lookout, 3km W of Paluma, 13.i.1970, at light, EB, Misko, 2♂ (ANIC). 19.00S,146.12E, Mt. Spec, 1.1966, GB, 6♂. Mt Spec, via Paluma, 8.xii.1965, GBM, 1♂ (UQ); 17.xii.1966, BC, 5♂ (UQ). 19.05S,146.20E, Paluma, 7.xii.1964, LP & GBM, 22♂, 1♀, 3 larvae (T.122), 17.i.1970, in RF, EB, 2♂ (ANIC). Ewan Road, Paluma, 9.i.1968, GB, 1♂. Paluma, Mt Spec, at light, 5.i.1966, GB, 11♂. Paluma Dam, 26.xii.1963, GBM, 24♂ (3♂ T.6, UQ); 30-31.xii.1964, GBM, 1 larva (T.131). Birthday Ck, via Paluma, 4.i.1973, BC, 1♂.

DIAGNOSIS. Male small to medium sized (5.5-10mm long); pronotum very pale cream with median dark marking; elytra dark brown, with interstitial lines 2, 3 and 4 dark brown, and broad pale cream lateral, apical and sutural borders; elytra slightly convex sided when closed; antennal sockets very close; frons-vertex junction not defined. Female macropterous, coloured as for male. Presumed larva with lateral tergal margins ridged.

DESCRIPTION. Males are redescribed; females and larvae are newly described.

Male. 5.5-10.0mm long (lectotype 8.7mm long); pronotum pale cream with median dark brown marking (Fig. 1F); anterior margin of pronotum to either side of midline may be narrowly dark; MS and MN pale; elytra very dark, almost black, with a broad marginal pale cream band extending around elytra except across base; in older specimens the dark elytral colour is restricted, either to an area wholly contained within the dark interstitial lines 1-3, or contained between dark interstitial lines 2-3, with a basal and apical brown area between lines 1, 2 and the intervening area pale blotchy brown, or restricted to the basal 1/8 of elytra, where the interstitial lines are also dark, and the remainder of the elytron including the interstitial lines is pale; interstitial lines 1-3 wholly within dark area, 4 wholly within the lateral cream margin; ventral pronotum dark margined around head cavity; head, antennae and palpi dark brown; frons may be paler than rest; apical segments of maxillary and labial palpi may be pale on their inner margins; ventral pro and mesothorax pale marked with brown, metathorax entirely dark brown; legs dark brown except for pale trochanters, and sometimes pale coxae 2; abdomen black except for pale sternites 6, 7 and tergite 8, and pale tergite 7 with brown markings (Fig. 3F,I).

Pronotum (Fig. 1F) 2.3-3.0mm wide; 1.3-1.7mm long; W/L (lectotype) 2.0; midanterior margin sometimes ridge like, moderately produced beyond anterolateral angles; mid-anterolateral margin may be slightly indented; lateral margins divergent posteriorly; punctures broad, shallow, contiguous. Elytra slightly convex-sided when closed; with 4 well defined interstitial lines, of which 1 is the longest, and 4 usually the shortest; lines 1, 2 sometimes subequal in length and almost as long as 4.

Head (Fig. 2H) not completely covered by pronotum at rest, deeply depressed between eyes; GHW 1.4-2.0mm; SIW 0.2-0.3mm; antennal sockets contiguous or nearly so; frons 1 × ASW, sloping gently to vertex, no defined frons-vertex junction; mouthparts small; apical segment of labial palpi flattened and dentate. Antennal length slightly > GHW; FS 1, 2 subequal, and slightly longer than remainder; FS 3-5 subequal in length, and broader than FS 6-8, which are subequal in length; FS 9 elongate slender, about 1.5 × FS 8.

Light organs occupying sternites 6 and 7 entirely (Fig. 3F,I); MPP of sternite 7 barely produced and gently rounded; tergite 8 with lateral margins subparallel, median posterior margin rounded and projecting a little beyond the rounded posterolateral corners. Aedeagus (Fig. 5D-F) L/W 3; basal piece not hood like; ML not bulbous around ejaculatory orifice or apex; LL sub parallel sided, narrowing slightly in apical

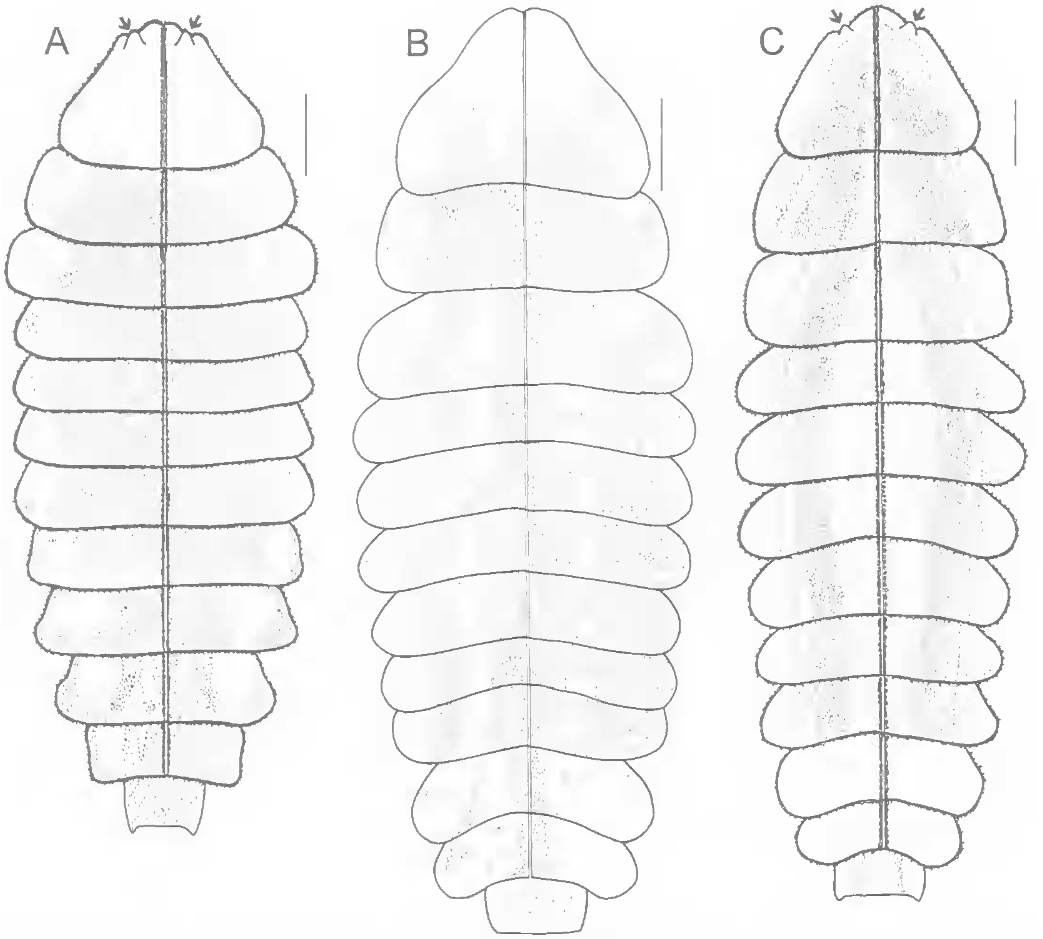

FIG. 15. *Atyphella* larvae, dorsal aspects. A, *A. olivieri*; B, *A. lychnus* (left and right sides represent different colour patterns); C, *A. scintillans*. Arrows indicate pronotal tubercles. Scale lines 1mm.

1/3, and gently diverging at apex; hairs borne in apical 1/3 or less.

Female. 6.5-8.0mm long; elytra fully developed but not covering gravid abdomen and at least 3 sternites may protrude beyond tips of elytra; hind wings almost as long as elytra, and gravid female may not be capable of flight. Coloured as for male with these exceptions: all legs light brown; ventral thorax cream with extensive light brown markings; abdomen pale cream with pale light organ in sternite 7.

Pronotal outline like that of male except midanterior margin narrowly indented, and midposterior margin broadly and shallowly indented. Head of winged female head form; with small mouthparts; GHW 2-2.5 × SIW; slightly depressed between the eyes. Abdomen with median posterior margins of sternites 7 and narrowly indented.

Larva. Larvae not reliably associated; taken at the same time as numerous flying males (LB, pers. obs.) (Fig. 15).

All terga with lateral margins thickened and all dorsal surfaces including margins bearing numerous minute spines and hairs, especially densely across posterior margins of terga; median line from anterior margin of tergum 1 to posterior margin of tergum 11 elevated and laterally ridged; punctures in anterior half of terga 2-10 not any larger than rest. Protergum midanterior margin indented; specimens # have a small dorsal elevation in the median area 1/4 length of pronotum behind the anterior margin; anterolateral areas of protergum indented and bearing paired rounded tubercles of which one pair projects dorsally and one pair ventrally; posterolateral corners of all terga except 12 rounded; posterolateral corners of 12 projecting slightly. Head broadly and shallowly excavated across anterior margin.

Dorsum yellow, with extensive dark brown markings; protergum yellow with brown lateral margins and midline brown margined; terga 2-8 dark brown with lateral areas cream; terga 10, 11 with extensive cream areas; terminal tergum dark brown; ventral surface cream with extensive dark markings; legs cream to light brown; thoracic epipleural plates dark brown; ventral plates of abdominal sterna 4-9 dark brown, with irregular cream markings on epipleural plates, and a narrow median cream area on sternal plates; epipleural plates of segment 10 margined with brown, remainder of segments 10-12 cream.

DISTRIBUTION. Occurs from sea level to above 1,000m throughout the Wet Tropics zone of N Qld and is one of the few species to occur at Paluma Ra. in the southern sector (Fig. 16).

REMARKS. This easily recognisable species is well represented in collections, flies in large numbers and is easily netted at night (LB, pers. obs.). It is frequently taken with either *A. inconspicua* or *A. brevis*. A living specimen is shown in Fig. 36A. Certain (?older) specimens have paler elytral colouration which has caused them to be identified in collections as *A. flammans*.

Atyphella scintillans Olliff
(Figs 1, 5, 15, 36C)

Atyphella scintillans Olliff, 1890: 650. Lea, 1909: 111; 1921a: 198 (female). Ballantyne in Calder, 1998: 177 (comb. rev.).
Luciola decora Olivier, 1902: 77; 1907: 51; 1910: 47. Lea, 1909: 111 (synonymy).
Luciola (Atyphella) scintillans (Olliff). McDermott, 1964: 44.
Luciola (Luciola) scintillans (Olliff). McDermott, 1966: 112.

TYPE. Lectotype. ♂ (designated here). NSW: Ash I., Upper Hunter R, Scott (specimen on the right of 2 syntypes glued ventral side down on card) (K33980, AM). Paralectotypes, 4♂ labelled as for lectotype (AM, SAM).

MATERIAL. Lectotype, paralectotypes and 231 specimens. SE QLD: 24.32S, 151.23E, Bulburin SF 600m, 9km E of Many Peaks, 17.ix.1989, GBM, 1♂ (QM). 26.51S, 151.34E, Bunya Mtns, x.1919, H. Carter, 1♂, 1♀ (MV); 18-19.xi.1967, GBM, 1♂ (UQ), 1♂ (QM); 21.ii.1965, GBM, 1 larva (T.158, UQ); 3♀ (SAM); 16.x.1973, A. Neboiss, 4♂ (MV); 10.xii.1925, HH, 1♀ (QM); 8.x.1968, flashing at night, T. Houston, 1♂ (SAM). Mt Nebo iv.1984, M. Peterson, 1♂ (ANIC). Moss' Well, Spicer's Gap, 13-14.x.1984, R. de Keyser, 3♂. 27.28S, 153.01E, Brisbane, May, 1959, 2 larvae, E. Bernays (T.37 UQ); 1.v.1961, 1♂, 9.iv.1960, 1♂, K. Korboot; 5.ix.1962, E. Bernays, 1♂; 20.ix.1962, 2♂ B. Wilson; 20.xi.1963, P. Shepherd, 1♂; 5.x.1973, A. Burrows, 1♂. Brisbane, University Mine site at Indooroopilly, LP, ix-x.1962, 4♂, 2♀, 4 larvae (2♂, 1♀ T.34, 1♀ T.35, 4 larvae T. 38,39). 27.20S, 152.46E, Mt Glorious, 24.ix.1963, GBM 2 larvae (T. 85,86); 16.viii.1964, TW, 1 larva (T.90); 14.x.1994, K. Hiller, 4♂, 1♀ (QM). Mt. Glorious, Maiala NP, in lantana, 6.30 p.m., 20.ix.1964, LP, 2♀ (both had laid eggs before preservation, T.97 UQ). Highvale, 5.x.1963, A. French, 1♂. 27.30S, 152.55E, Brookfield, 20.ix.1964, 1♂ (T.89). 27.91S, 153.16E, Mt Tamborine, Joalah NP, 23.vii.1979, JL, ANIC berlesate 656 flood debris and leaf litter, 2 larvae

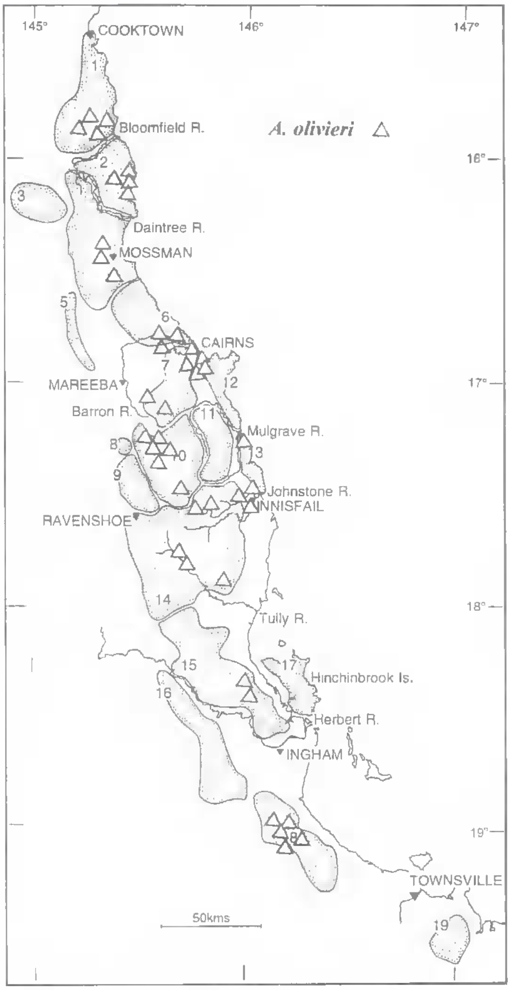

FIG. 16. Records of *Atyphella olivieri* in far north Queensland rainforest.

(ANIC). 28.03S, 152.24E, Cunningham's Gap NP, 26.xi.1964, LP, 8♂, 1♀(5♂, 1♀ T.155, UQ); 30. xi.1963, in leaf mould, GBM, 1 larva (T.36); 26.xi.1964, H. Rose, 1♂; 12.vi.1961, J. Barrett, 1 larva, (T.65); 1953, GB, 4♂ (ANIC). 28.05S, 153.27E, Burleigh Heads NP, 1961, A. Hiley, 1♂ (UQ); 29.vii.1961, LP, 1♂ (T.64); 20.xii.1963, LP, 7 larvae (T.33); vii.1961, R. Winks, 1♂; 3.ix.1940, HH, 2♂ (BMNH), 2♂ (QM). 28.19S, 153.05E, Lamington NP 19.ii.1961, N. Heather, 1♂ (UQ); 22.v.1962, J. Ferguson, 1♂; 25.v.1962, A. May, 1♂; 11.x.1959, I. Yeo, 2♂; xii.1921, HH, 2 larvae (Lea 1929 tentatively identified these as *A. brevis*); 25-26.x.1923, HH, 19♂ (QM); xii.1921 HH, 2 larvae (identified by Lea 1929: 345 as possible *A. brevis*); 2km N of O'Reilly's, in RF in showery but warm weather, 31.xii.1982, P. Harris, 2♀ (T.255 UQ). Cedar Ck, 28.ix.1930, HH. 7♂ (QM). 28.33S, 152.36E, Queen Mary Falls, Killarney, 12.x.1973, A. Neboiss, 1♂ (MV). NSW: 28.10S, 153.33E, Tweed Heads, J. Follent, 1.ix.1949, 1♂ (QM). 28.10S, 152.36E, 20kms NE of Legume, flying at night, 5.xi.1981, S. Barker, 10♂ (SAM). 28.28S, 152.33E, Tooloom Plat, via Urbenville, 31.x.1970, GBM, 12♂ (UQ); 29-30.x.1982, GBM, 2♂ (QM). 28.27S, 152.45E, Unumgar SF, 580m nr Grevillea, Cox's Road 789, 2-11.i.1987, A. Newton, M. Thayer, subtropical RF, FMHD # 87-177 berlesate, leaf and log litter, 2 larvae (ANIC). 28.40S, 152.21E, Clarence R, 3♂ (MM); ix.1904, H. Carter, 4♂ (MV). Upper Clarence R, ix.1904, H. Carter, 2♂. 28.50S, 153.26E, Victoria Park, via Alstonville, 1.xi.1970, GBM, 1♂ (UQ). 30.64S, 153.01E, Nambucca Heads, 8.ix.1966, G. Condon, 1♂ (AM). 31.35S, 152.36E, junction of Myrtle Rock Road and Compartment 81, Kerewong SF, E of Comboyne, 17.x.1979, stop 39, D. & B. Rentz, 1♂ (ANIC). 32.04S, 151.41E, Gloucester R., Barrington Tops NP, 12-14.xi.1981, TW, 7♂. Barrington House via Salisbury, 26-28.xii.1965, BC, 1 larva. 32.06S, 151.29E, Upper Williams R, Lea, Wilson, 19♂, x.1926 (SAM), 3♂ (UQ), 2♂ (MM); 4♂ (ANIC); 5♂ (MV). William's R, x.1925, H. Carter, 3♂ (ANIC). nr Cutter's Pass, William's R, A. Musgrave, T. Campbell, 23-30.x.1926, 10♂ (AM). 32.08S, 151.27E, Allyn R nr Chichester SF, 10-11.xi.1981, TW, 1♂ (ANIC). 32.13S, 151.34E, Barrington House, via Salisbury, 26-28.xii.1965, BC, 8 larvae (T.192 UQ). Salisbury, 1-5.xi.1957, F. Perkins, 3♂. Barrington, E. Davies, 2♂ (MV). Acacia Plat, 20.xi.1955, J. Sedlacek, 1♂ (UQ), 2♂ (BPBM). 32.13S, 152.51E, Forster, 29.ix.1993, A. Rose, 3♂ (AM). 32.15S, 151.20E, Tuglo Wildlife Refuge, 17.xi.1985, B. Day, 1♂. 32.17S, 152.50E, Cape Hawk, C. Burett, 2♂ (MV). 34.54S, 150.00E, Wilson Park, 50m, 3km SE of Lismore, S. & J. Peck, dry RF litter, 2 larvae (ANIC).

DIAGNOSIS. Male medium sized (6.6-9.9mm long); pronotum cream with median dark marking; elytra black with 4 well defined interstitial lines; elytra parallel-sided when closed; antennal sockets not contiguous; frons-vertex junction convex. Female with greatly shortened elytra which are contiguous in the mid line, and vestigial hind wings; dorsally cream except for median brown marking on pronotum. Larva (Fig. 15) dorsally brown, marked in dark brown, black, and yellow.

DESCRIPTION. Males and females are redescribed; larvae are newly described.

Male. 6.6-9.9mm long (lectotype 8.5mm); pronotum cream with median dark markings; MS brown, anterolateral corners sometimes pale; MN cream; elytra very dark brown; head and antennae very dark brown; ventral prothorax cream, mesothorax cream with brown markings, and metathorax dark brown with lateral margins pale; legs 1, 2 cream with dark tibiae and tarsi; legs 3 cream with coxae, tibiae and tarsi dark brown; abdominal sternites black except for cream 6, 7; tergites 2-5 dark brown, 6 and 7 light brown (Bulburin male in QM has 6 and 7 dark brown); 8 pale cream.

Pronotum (Fig. 1C) 2.1-3.4mm wide; 1.3-1.7mm long; W/L (lectotype) 1.6; midanterior margin bluntly pointed; lateral margins diverging posteriorly; punctures small, not contiguous over centre of disc, larger and contiguous in lateral and postero-median area. Elytra parallel-sided when closed; with 4 well-defined interstitial lines.

Head concealed beneath pronotum at rest; deeply depressed between eyes; GHW 1.4-2.0mm; SIW 0.25mm; ASD subequal to or > ASW; scarce frons, about 1 × ASW, frons-vertex junction well defined, convex; mouthparts well developed; apical segment of labial palpi fusiform. Antennae apparently 9 segmented, (10 segmented in Bulburin male in QM); antennal length slightly < GHW; FS 1 1.5 × FS 2, and acutely narrowed basally; FS 3-5 subequal, and slightly shorter than 1, 2.

Light organs occupying sternites 6, 7 except for a narrow posterior margin of 7; MPP of sternite 7 slightly produced; lateral margins of tergite 8 subparallel, median posterior margin rounded and projecting a little beyond posterolateral corners. Aedeagus (Fig. 5V,W) L/W 1.7 (lectotype); ML moderately expanded around ejaculatory orifice, scarcely expanded at apex; LL subparallel to slightly convex along lateral margins, divergent along their length dorsally, bulbous at apices.

Female. 5.5-11.0mm long; brachelytral, hind wings present as narrow vestiges. Dorsal body pale cream except for dark median markings on pronotum, and light brown elytra; head, antennae and palpi light brown; light organ in sternite 7 waxy white.

Pronotal outline like that of male. Elytra 1.5 × as long as median length of pronotum, contiguous in midline, and with 4 moderately well defined interstitial lines present. Head of wingless female form; GHW 2-3 × SIW; shallowly depressed between eyes; antennae 9 segmented. Abdomen with median posterior margins of sternites 8 and 9 narrowly emarginate.

Larva. (Fig. 15C). Lateral margins of terga 1-11 moderately strongly ridged and clothed with short hairs and short stout spines; median line from anterior margin of tergum 1 to posterior margin of tergum 10 bordered by large elevated punctures; punctures across anterior median fifth of terga 2-11 much larger than rest. Protergum 1.0-2.0mm long, 1.7-3.0mm wide; median anterior margin slightly indented; tubercles present, dorsal pair more strongly developed than ventral pair; posterolateral corners of protergum and terga 2-11 rounded. Posterolateral corners of tergum 12 scarcely produced. Median anterior margin of head broadly and shallowly indented (Fig. 7O).

Dorsally brown-very dark brown and yellow; protergum cream, margined with brown, and extensively marked in brown in posterior half; terga 2-5 similarly marked, mostly brown, with broad very dark bands extending from anterior to posterior margins and narrowly yellow immediately outside these dark bands; thoracic terga 2, 3 usually darker than abdominal terga; abdominal terga 8, 9 may be darker than preceding terga; terga 10, 11 almost entirely yellow, except for brown margin; tergum 12 dark brown with anterolateral areas cream; ventral body yellow or cream with scattered faintly dark markings.

DISTRIBUTION. SE Qld and NE NSW in rainforest or remnant rainforest, especially in suburban Brisbane; often coastal (Fig. 17).

BIOLOGY. *Atyphella scintillans* has been taken in February, September and November from areas near the Brisbane R in Indooroopilly and Corinda, former rainforest areas then supporting dense lantana. In the 1960s a hill slope behind the University experimental mine at Indooroopilly provided a relatively undisturbed area for studying this species and *Luciola nigra*, which often flew together. The males of *A. scintillans* flew for about an hour just after dusk. Flight time varies according to weather conditions (e.g. very short in September if nights were cold. Adults did not fly after a very windy day). The brachelytral females were only taken on the ground if their slow and regular flashing was recognised. Living males and females are shown in Fig. 36C. Larvae, recognised by their continuous glow, were collected in moister pockets on the ground. The larval light was continuous unless disturbed, then gradually faded to extinction (Powell, 1964).

REMARKS. Olliff (1890) described the antennae of *Atyphella scintillans* as similar to those of *A. lychnus*, except for the larger terminal joint. *A. scintillans* has only 9 antennal segments. Lea (1921a) described the female from specimens taken with males. McDermott (1964: 44) referred to the female as brachelytral and larviform.

Atyphella similis Ballantyne sp. nov.
(Figs 1, 4, 5, 12)

TYPE. Holotype. ♂, S Qld: 28.19S, 153.05E, Lamington NP at Binna Burra Lodge, 2-3.xii.1965, S. Curtis and LP (QMT T62936).

MATERIAL. Holotype and 509 paratypes. SE QLD: same data as holotype, 197♂ (UQ); v.1962, LP, 80 larvae (T. 2, 3, 59, 100); 11-24.v.1965, GBM, 8 larvae (T.193); 9.xii.1962, LP, 13♂, 2♀, (2 ♂, 2 ♀ T.1), 4 larvae (ANIC). Lamington NP: 4♂, R. Illidge (UQ); xii.1919, HH, 1♂ (QM); xii. 1921 HH, 2♂ (QM, 2♂, 2 larvae are mounted on one card, id. *A. brevis* by A. Lea; the larvae are *A. scintillans*); 2km N of O'Reillys, 31.xii.1982, P. Harris, 2 females (T.255 UQ); nr O'Reilly's, 4.iii.1980, JL, ANIC berlesate 673 leaf litter, 2 larvae (ANIC). 27.55S, 152.26E, Gatton, 19.ii.1961, A. Hiley, 1♂ (UQ; loc. requires confirmation). 27.91S, 153.16E, Mt Tamborine, 4♂ 20.xi.1925, HH (QM. id as *A. lychnus* by A. Lea); Joalah NP, 23.vii.1979, JL, ANIC berlesate 656 flood debris and leaf litter, 4 larvae (ANIC); 20.x.1978, berlesate 653, litter, JL, TW, 9 larvae. Mt Tamborine, N side nr Curtis Falls, leaf mould in RF, 8.v.1953, T. Woodward, 5 larvae (T.60 UQ). 28.06S, 152.24E. Spicer's Peak summit, 30-31.xii.1993, 1200m, GBM, 1♂ (QM). Lever's Plat via Rathdowney, 4.iv.1966, GBM, 7 larvae (T.162 UQ). 28.28S, 152.70E, Barney, 13.xii.1964, S. Curtis, 7♂ (T.204). NSW: 28.23S, 152.46E, Mt Glennie, 16km E of Woodenbong, 25.xi.1982, sieved litter in RF, 910m, GBM, DY, DC, 1♂ (QM). Mt Glennie, 16km E of Woodenbong, 25.x. 1982-3.ii.1983 Q Mus RF FIT, 910m. 11♂ (QM). 28.24S. 152.40E, Unumgar SF, 430m nr Woodenbong, Pole Bridge Road 788, 2-11.i.1987, A. Newton, M. Thayer, dry RF Araucaria-Eucalyptus, FMHD #87-174 berlesate leaf and log litter, 1 larva (ANIC). 28.31S, 153.17E, Nightcap NP., 700m Googarna Rd 3km N of Mt. Nardi 790, 4.i.1987, A. Newton, M. Thayer, warm temperate RF, FMHD #87-178 berlesate, leaf and log litter, 4 larvae. 28.37S, 152.25E, Tooloom Scrub, 30.xii.1966, GBM, 25♂ (T.209). 28.51S, 152.96E, Wiangaree SF, 1000m, 33km NE of Wiangaree, S. & J. Peck, 24.viii.1982, *Nothofagus* litter, 7 larvae (ANIC); 600m, Sheepstation Ck, 29.ii-3.iii.1980, subtropical RF, 26 larvae; Brindle Ck 740m, berlesate from log and leaf litter, 50 larvae. 29.29S, 152.46E, Toonumbar SF 770m, nr Grevillea, Murray Scrub 794, 6.i.1987, A. Newton, M. Thayer, subtropical RF, FMHD #87-182 berlesate leaf and log litter, 7 larvae (ANIC). 29.36S, 152.11E, Gibraltar Ra., via Glen Innes. 27-19 .xii.1972, in RF, GBM, 3♂ (UQ). 30.20S, 152.34E, Dorrigo, 15.xii.1911, R. Tillyard, 4♂

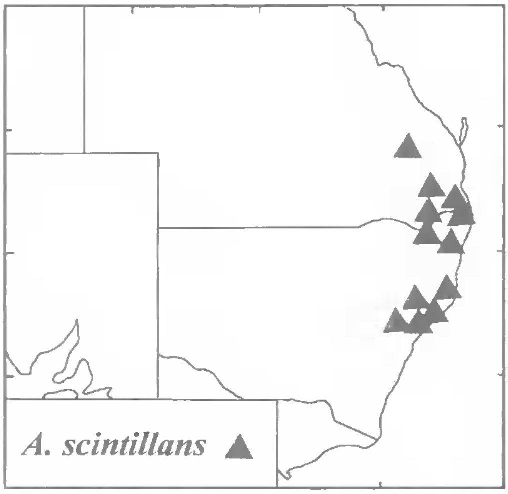

FIG 17. Records for *Atyphella scintillans* in southeast Australia.

(QM); 1♂ (MV, identified as *A. lychnus* by A. M Lea); W. Heron, 3♂ (ANIC). Ulong, E Dorrigo, W. Heron, 2♂ (AM). 30.23S, 152.44E, Dorrigo NP, c. 5km SSE of Dorrigo, 4.i.1971, K. Key, 1♂ (ANIC). Dorrigo NP, Never Never area, Sassafras Ck, wet temperate RF, 750m, 7.xii.1992. D. Bickel, 1♂ (AM). 30.30S, 152.23E, Wright's lookout track, New England NP, 16-18.xi.1990, TW, ANIC berlesate 1131, RF litter under *Nothofagus moorei* and *Dicksonia antarctica*), 5 larvae (ANIC). 30.38S, 152.12E, Styx R SF, 31.xii.1992, V. Lorimer, in detritus, fern tree, 1♂ (AM). 34.54S, 150.00E, Raspberry Rd on Big Hill, 40m E of Armidale, xii.1971, R. Hardie, 4♂ (ANIC).

DIAGNOSIS. Males small to medium (5.8-7.5mm long); pronotum cream with median dark markings; elytra parallel sided when closed, light brown with suture and 3 interstitial lines often paler. Females with very abbreviated elytra not contiguous in the midline, and no hind wings. Confused in collections with *Atyphella lychnus* Olliff and *A. atra* Lea, distinguished by the elytral and terminal abdominal tergite colouration, presence of only 3 elytral interstitial lines in the male, the distance separating the antennal sockets, the brachelytral female and the larval colouration. Very similar to *A. conspicua*, most obviously distinguished by its southern distribution, the width of the antennal sockets, colour of abdominal tergites 7 and 8, and the shape of the frons-vertex junction.

DESCRIPTION. *Male*. 5.8-7.5mm long (holotype 7.3mm long); pronotum cream with dark markings in anteromedial 2/3; MS and MN cream; elytra light brown, suture, lateral margin and interstitial lines often paler; elytra semitransparent and hind wings and body outlines may confuse true colour; head and antennae dark brown; ventral surface of pro and mesothorax pale, of metathorax brown; legs cream except for brown apical one-fifth of femora, and brown tibiae and tarsi; ventral surface of abdomen dark brown except for cream sternites 6 and 7; tergites 2-6 dark brown, 6 brown with cream median area, and 7 & 8 pale, semitransparent.

Pronotum (Fig. 1I) 1.7-2.6mm wide; 1.0-1.5mm long; W/L holotype 1.8; midanterior margin slightly acute or rounded, moderately produced beyond anterolateral angles; lateral margins slightly divergent posteriorly; punctures broad, shallow, contiguous over most of disc, punctures in median area of disk smaller, shallower and often separated by 1-2 width of puncture. Elytra parallel-sided when closed, with 3 well-defined interstitial lines (1, 2, and 4).

Head almost concealed beneath pronotum at rest, deeply depressed between the eyes; head between eyes very smooth and shiny; GHW 1.2-1.6mm; SIW 0.2-0.3mm; ASD = half or less than half ASW, never contiguous; frons 2-3 × ASW; frons-vertex junction acute but not elevated in median line; mouthparts moderately well developed; apical segment of labial palpi fusiform. FS1 half as long again as FS2, FS2-3 subequal in length, slightly longer than wide; FS 4-8 subequal in length, about as long as wide, FS 9 apically rounded, one and one-half times as long as FS 8.

Light organs occupying sternites 6 and 7 except for narrow posterior margin of 7; MPP of sternite 7 moderately produced and apically rounded and may be very slightly emarginate; tergite 8 subparallel sided in anterior half (Fig. 4A,D). Aedeagus (Fig. 5S-U) L/W 2.2; basal piece not hood like; ML not expanded at tip nor at level of EO; LL subparallel sided and markedly divergent in apical 1/5; hairs borne in apical 1/3.

Female. 5.5-8.0mm long; brachelytral; hind wings absent. Dorsally pale cream, pronotum dingy cream with median dark markings; elytra very pale brown; head, antennae and palpi light brown; venter of body cream, light organs in sternite 7 white.

Pronotum with midanterior margin rounded, slightly indented in median line; lateral margins slightly divergent in anterior 2/3 and convergent in posterior 1/3; disc scarcely depressed; punctures broad, shallow, some contiguous, some separated by width of puncture; posterolateral corners may be slightly produced. Elytra half as long as pronotum, lacking interstitial lines; sutural margins not touching in repose, not reaching lateral margins of MS in repose. Hind wings absent.

Head of wingless female form; GHW = or slightly < 2 × SIW; ASD > ASW; gently depressed between eyes; frons-vertex junction ridge like.

Median posterior margin of terminal abdominal sternite broadly emarginate, of penultimate sternite entire.

Larva. (Fig. 12B). Lateral margins of terga clothed in fine short hairs and spines, not strongly ridged; median line from anterior margin of tergum 1 to posterior margin of tergum 11 not ridged or margined; punctures in anterior half of terga 2-10 slightly larger than remainder. Protergum 1.1-2.3mm wide; 0.6-1.5mm long; median anterior margin slightly indented; lacking tubercles; posterolateral corners of protergum and thoracic and abdominal terga 4-9 rounded, of terga 10, 11 somewhat acute. Head with median anterior margin broadly and shallowly excavated.

Dorsal colouration cream with brown markings; either dingy cream with faint light mottling; or moderately dark brown , with paler markings; protergum with extensive anterolateral and lateral cream areas; terga 2-9 with pale anterolateral, lateral and posterolateral areas; terga 2-7 with median pale areas; abdominal terga 10 and 11 cream with mottled brown markings; ventral aspect of thorax mainly cream, all plates margined with brown; legs light brown; abdominal epipleural plates 4-9 dark brown, with inner margins cream, and plates 10, 11 cream; median ventral plates of segments 4-7 mainly cream with faint brown markings; abdominal sternum 8 quite extensively brown marked; ventral surface of abdominal segments 10-12 cream.

DISTRIBUTION. SE Qld and NE NSW in high cool mountain areas, mostly in RF; the wide distribution in NSW is based on larval and adult records (Fig. 18). A single record from Gatton is probably a mislabelled student collection.

REMARKS. It was surprising to find large numbers of a new lampyrid species in such a well-collected area as Lamington NP. It is similar to *Atyphella lychnus* Olliff and has been confused with that species, which is known from only two Queensland records. The specific name (Latin, *similis* = like, resembling) emphasises this similarity. The larva illustrated in Lawrence & Britton (1999: 639, fig. 35.391) is probably this species.

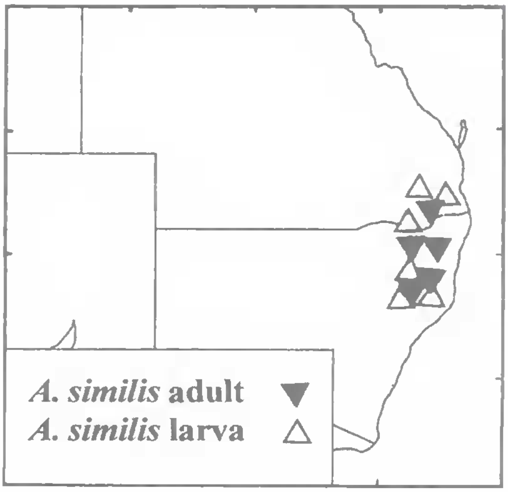

FIG. 18. Records for *Atyphella similis* in southeast Australia.

It was taken at Binna Burra flying in large numbers. Females on the ground were recognised by their slower rhythmic flashing in response to the aerial males. Larvae were taken when their light was sighted.

Luciola Laporte

Calder (1998) gave a full taxonomic history of this genus.

DESCRIPTION. MALE. Dorsal surfaces usually conspicuously punctate and moderately pubescent.

Pronotum. Width/length = 1.2-2.0; midanterior margin rounded, often projecting beyond the rounded, slightly obtuse anterolateral corners; lateral margins narrowly flattened, not more greatly expanded in posterior half in *L. australis, flavicollis, nigra, orapallida*; flattened and expanded more in posterior half in *L. cowleyi*; lateral margins subparallel, or converging a little anteriorly and posteriorly or divergent posteriorly at least in their anterior half, or convergent posteriorly; posterolateral corners approximately right angled, or rounded, obtuse and projecting slightly beyond posterior margin in *L. dejeani;* disc mostly convex, depressed around margin.

Elytra. Punctation not large; conspicuous and similar to that of pronotum; lacking deflexed apex; sub-parallel-sided when closed; at most 3 feebly developed interstitial lines except in *L. cowleyi* where 1, 2 and 4 are well defined; apex of elytron rounded; epipleuron extends past elytral midpoint but not to apex; sutural ridge extends almost to apex except in *L. cowleyi* where it extends only half the length of the elytron.

Head. When viewed from above is moderately to greatly exposed; deeply depressed between the eyes except in *L. dejeani*; posterolateral eye excavation slightly developed to markedly so; GHW 2-6 times SIW; labrum broader than long except in *L. cowleyi* where it is about as long as broad; antennal sockets never contiguous, always separated by at least half ASW; no well defined frontal area or frons-vertex junction; eyes contiguous or nearly so ventrally in *L. cowleyi*, moderately separated in all others. Mouthparts well developed and functional; apical segment of labial palpi fusiform except in *L. dejeani* where it is flattened and dentate. Antennae length approximately twice GHW except in *L. cowleyi* where it is slightly < GHW; 11 segmented, segments simple; FS1 longer than pedicel; all FS at least twice as long as wide; apical FS not shortened and club-like, no FS produced laterally or flattened.

Legs. No femora and tibiae curved or swollen. MFC absent.

Abdomen. Posterior margin of basal abdominal sternites not recurved. Light organs occupying sternite 6, sometimes slightly retracted from lateral and posterior margins (may be a post-mortem effect); light organ may occupy all of sternite 7 except for a narrow clear posterior band, or may be restricted to the anterior half or less. Sternite 7 MPP always developed, scarcely produced, wider than long and apically rounded in *L. dejeani*, sometimes conspicuously produced, often apically emarginate; MPP never upturned or engulfed by the downturned apex of tergite 8; posterolateral corners of sternite 7 rounded or angulate, not produced posteriorly; posterior margin lacking incurving lobes, pointed projections, median carina, median trough and dimple; posterior half of sternite 7 not arched or swollen. Tergite 8 symmetrical, not wider than long, projecting to or just extending beyond the posterior margin of sternite 7; median posterior area not narrowed, downturned and engulfing the MPP; ventral surface lacking lateral ridges and flanges in *cowleyi*; with lateral ridges and no flanges in *australis*, *flavicollis*, *nigra* and *orapallida*; tergite 8 pale in *australis*, *dejeani* and *orapallida*, dark brown or black in *flavicollis* and *nigra*.

Aedeagal Sheath. Symmetrical, lacking lateral protuberances of tergite, with anterior half of sternite 9 elongate, narrowed and symmetrical; sheath elongate, slender and symmetrical in *cowleyi*, *nigra*, *australis*, *flavicollis*; posterior half of sternite 9 symmetrical, and extending as far as posterior margin of tergite 9 in *nigra*, *australis*, *flavicollis*, posterior half of sternite shortened in *orapallida*, and narrowed, apically emarginate and not reaching to posterior margin of tergite 9 in *cowleyi*; tergite 9 slender tapering posteriorly and scarcely visible. Aedeagus elongate and slender in *nigra*, *australis*, *flavicollis* and *orapallida*, with ML narrow at apex, slightly longer than LL which narrow towards their apices and are separated and closely approximate along their dorsal length; apices of LL not visible from below; in *orapallida* the LL are widely separated but not divergent at narrowed apices; in *cowleyi* the ML is considerably shorter than the LL which are expanded in their basal 1/2 -2/3 and contiguous ventrally, and narrowed and widely separated in their apical 1/4-1/2; apices of LL are visible from above and below and bear small hairy lobes along their inner ventral surface; in *dejeani* the ML is subequal in length to the LL which are as broad at their apices as at their bases, and bear elongate narrowed flaps along their inner ventral surface.

FEMALE. Macropterous.

Pronotum. Outline similar to that of male, but anterolateral angles usually more rounded and midanterior margin often not much produced beyond anterolateral angles.

Elytra. Interstitial lines feebly developed.

Head. Small, concealed beneath pronotum at rest; shallowly depressed between the eyes, GHW 2-5 × SIW; mouthparts well developed; antennal length always slightly longer than GHW. Light organ material restricted to the ventral surface of sternite 6 only; sternites 7 and 8 tapering posteriorly, and often medially emarginate.

LARVA. Lacking laterally projecting acute tergal margins; legs with tarsal claw about 1/3 as long as tibiotarsus.

REMARKS. *Luciola* (*sensu* McDermott, 1966) is widely distributed throughout Europe, Asia and the Pacific and its morphological diversity was discussed by Ballantyne (1968). It is an heterogeneous assemblage which McDermott (1964), Ballantyne & McLean (1970) and Ballantyne (1968, 1987a, 1987b) all considered to be in major need of revision. This need is supported by the following phylogenetic analysis.

Luciola is redescribed here from Australian species identified as species groups in the cladistic analysis, and comprises 3 distinctive groups: i) *dejeani* (which may not be Australian); ii) *cowleyi*; iii) an Australian and New Guinean element of *australis*, *flavicollis*, *nigra* and *orapallida* sp. nov. *Luciola dejeani* is known from one Australian record and *L. cowleyi* from isolated records across the Gulf of Carpentaria and 'NW Australia', except for a sole record of *cowleyi* from Kuranda, which is probably incorrect. Similarities with African and Indian species are discussed later for both of these species. Of the remaining category *flavicollis* and *nigra*, which also occur in New Guinea (Ballantyne, 1992), are widely distributed along the eastern seaboard of Queensland as far south as Brisbane.

KEY TO MALES OF AUSTRALIAN *LUCIOLA*

1. Dorsal surface pale yellow, with elytral apices black . . . . *dejeani* Gemminger

   Dorsal surfaces variously coloured but never entirely yellow with only the elytral apices black 2

2. Median posterior margin of sternite 7 either not produced, or at most slightly produced and apically rounded or slightly emarginate, with lateral margins converging posteriorly 3

   Median posterior projection of sternite 7 considerably produced posteriorly, apically emarginate or truncate, with lateral margins subparallel sided 4

3. Underside of thorax (excluding legs) and/or abdomen (except light organs) always with some dark brown to black markings; pronotum with median dark markings; posterolateral excavation of eyes pronounced and clearly visible when head is in withdrawn condition; median posterior margin of sternite 7 not produced . . . . *cowleyi* Blackburn

   Underside of thorax (excluding legs) and abdomen (excluding light organs) pale yellow; pronotum yellow, lacking dark markings; posterolateral excavation of eyes not pronounced and not visible when head is in withdrawn condition; median posterior margin of sternite 7 a little produced, apically rounded or emarginate . . . . *australis* F.

4. Elytra very dark brown with no paler markings; ventral surface black except for pale light organ in sternites 6, 7 . . . . *nigra* Olivier

   Elytra pale to dark brown, always with paler markings either at base and/or along lateral and/or sutural margins; ventral surface not always entirely black except for white light organs 5

5. Elytra brown, with bases and apices brown, and lateral margins widely pale; most of ventral surface of body pale; aedeagus (Fig. 21O-Q) with lateral lobes very narrow and widely separated dorsally . . . . *orapallida* sp. nov.

   Elytra brown, always with some orange markings, either across base, and/or suture, and/or lateral margin; most of ventral surface of body very dark brown; aedeagus with lateral lobes closely approaching dorsally (Fig. 21U-W) . . . . *flavicollis* MacLeay

KEY TO KNOWN FEMALES OF AUSTRALIAN *LUCIOLA*

This key includes reliably associated females, all of which are macropterous, as well as a single female from Murray Is which is treated only as *Luciola* species A.

1. Body brown except for pale light organ in sternite 7 . . . . *Luciola* sp. A

   Body never all brown, at least pronotum pale orange . . . 2

2. Venter of body yellow, except for white sternite 6 and brown tibiae and tarsi; elytra dark brown, margins not paler than rest . . . . *australis* F.

   Venter of body dark brown except for pale light organs; or at least basal abdominal sternites dark brown; if ventral surface paler, then elytra with pale lateral and sutural margins 3

3. Elytra dark brown; margins no paler than rest . . . . *nigra* Olivier

   Elytra dark brown with some paler orange markings either at base or along lateral and sutural margins 4

4. Most of ventral surface of body and all of legs dark brown to black; elytra often pale orange yellow at base and/or narrowly pale margined laterally and along suture; sternites 8 and 9 black . . . . *flavicollis* MacLeay

   Most of ventral surface of body, and all of legs, yellow to pale brown; elytra brown at base and widely pale margined along lateral margin and suture; sternites 8 and 9 yellow. . . . . *orapallida* sp. nov.

KEY TO KNOWN SPECIES OF *LUCIOLA* LARVAE FROM AUSTRALIA

1. Tergum 1 bearing 6 well defined tubercles along anterior margin (Fig. 22A). . . . . *australis* F.

   Tergum 1 lacking well-defined tubercles along anterior margin (Fig. 22B,C) 2

2. All except terminal tergum with a wide pale median line and widely pale lateral margins (Fig. 22C) . . . . *nigra* Olivier

   All terga lacking a wide pale median band and pale lateral margins . . . . *orapallida* sp.nov.

Luciola (Luciola) australis (Fabricius)
(Fig. 22)

Lampyris australis Fabricius 1775: 201; 1781: 253; 1787: 162; 1792: 102; 1801: 104. Lacordaire, 1857: 338. Motschulsky, 1854: 53 (partim). *Nec* Guérin-Méneville, 1838: 74. Boisduval, 1835: 125, plate vi, fig. 13.

Lampyris italica var. *australis* Fabricius. Olivier, G., 1790: 18, Fabricius, 1792: 104.

Luciola australis (F.). Laporte, 1833: 150. Lea, 1909: 108 (partim). Masters, 1886: 288; 1888: 327. McDermott, 1966: 99. (partim). Ballantyne, 1988: 161. Calder, 1998: 178. *Nec* Gorham, 1880: 104; Olivier, 1883: 330; 1885: 362; 1902: 74 (larva); 1907: 50; 1909b: lxxxi; 1913: 417; Olliff, 1890: 652; Lea, 1921a: 197.

Luciola pudica Olliff, 1890: 652. Lea, 1909: 109 (female). McDermott, 1966: 112. Ballantyne, 1988: 162 (Synonymy).

TYPE. Lectotype. ♂, New Holland (designated by Ballantyne, 1988) in Hunterian collection, University of Glasgow (see below).

MATERIAL. Lectotype and 131 specimens. N QLD: Cape Pallarenda, Townsville, in mangroves, 8.xii.1964, LP, GBM, 5♂, 2♀, 10 larvae (T.120 UQ). Townsville, xi.1902, F. Dodd, 3♂ (SAMA). Ross R nr Townsville, 15-16.ix.1980, J. Case 4♂, 3♀ (ANIC). 18.16S, 146.01E, Round Hill Landing 15km SE of Cardwell, in mangroves, 7.xi.1984, GBM, DC, 1♂ (QM). Bowen, 1♂ (SAMA). CENTRAL QLD: 21.09S, 149.11E, Halftide nr Mackay, 8.ii.1965, to light, E. Dahms, 2♂, 1♀ (QM). Mackay, mouth of Baker's Ck, in mangroves, to light, 7.ii.1965, E. Dahms, 4♂, 3♀ (QM). 23.11S, 150.73E, Yeppoon, iv.1961, LP, 10♂, 1♀ (UQ). Tanby, nr Yeppoon, xii.1962, J. Frisch, 5♂ (UQ). Gladstone, 23.xii.1963, GBM, 1♂ (UQ). Port Denison, 1♂ (SAMA). Pacific Highway 14m S of Gladstone at Boyne R. crossing, in mangroves, netted in flight, LP, iv. 1961 5♂, 5♀, 6 larvae (T. 47-50 UQ); 1.i.1962 3♀; 24.xii.1962 2♂. S QLD: Bundaberg, 29.x.1972, H. Frauca, 3♂, 2♀ (ANIC). NSW. No other data, 1♂, 1♀ (MM).

DIAGNOSIS. Male 5.5-7.0mm long; pronotum orange, elytra very dark brown, ventral surface mostly yellow; eyes lacking any visible posterolateral excavation when head is withdrawn; MPP of sternite 7 rounded; sternite 7 lacking posterolateral projections; ventral surface of tergite 8 with lateral ridges and short pointed lateral flanges. Aedeagus elongate slender, ML longer than LL which taper to their apices. Female macropterous, coloured like male except pale light organ in sternite 7 only. Larva (Fig. 22A) with small rounded protuberances along posterior margins of terga.

REMARKS. Ballantyne (1988) resolved the identity of this species and redescribed males, females and larvae. *Luciola australis* F. was the only firefly species collected by Joseph Banks during the voyage of the 'Endeavour' in 1770. Radford (1981) recorded the existence of an apparent Fabrician type in the Hunterian (entomological) collection in the Department of Zoology at the University of Glasgow. In 1983 Dr Roy Crowson determined that one of the Hunterian specimens, a male, conformed to *L. pudica* Olliff, but that the other, identified by him as a female, did not conform and was not identified (Ballantyne, 1988). In October 1993 LB examined the 2 male specimens then standing under the label *Luciola australis* F. in the Hunterian collection. LB chose the specimen on the right as being closest to the original description of *L. australis*, but comparisons could only be approximate (legs and antennae are incomplete, and the ventral surface of the metathorax and abdomen is light brown, doubtless an effect of age). The crucial feature of the original Fabricius description is that of the underside of the body viz. 'subtus flavicans'. LB cannot determine the identity of the second specimen, which is a male and also incomplete, and may have been taken in Indonesia during the latter part of the Endeavour voyage (Ballantyne, 1992).

Ballantyne & Buck (1979) described features of the larva, and Powell (1964) aspects of the biology. With the exception of one label record from NSW (no specific locality was given and is probably mislabelled) it is known from Townsville to Bundaberg, usually in mangroves.

Luciola (Luciola) cowleyi Blackburn
(Figs 19, 21)

Luciola Cowleyi Blackburn, 1897: 34. Olivier, 1902: 76; 1907: 51. Lea, 1909: 108; 1921a: 197.

Luciola (Luciola) cowleyi Blackburn. McDermott, 1966: 102. Ballantyne, 1968: 125.

Luciola quadricostata Pic, 1938: 3. Ballantyne, 1968: 125 (Synonymy).

TYPES. Holotype. ♂, *Luciola cowleyi* Blackburn, Australia, N Qld (BMNH). Holotype♂, *Luciola quadricostata* Pic, North Australia (Natural History Museum, Basel).

MATERIAL. Two types and 56 specimens. NORTHERN TERRITORY: 12.27S, 130.50E, Darwin, W.K. Hunt, 19♂ (UQ; SAM; QM; BMNH; MV); G.F. Hill, 16♂ (ANIC, UQ, SAM, MV); 11-12.ii.1945, B. Malkin, 14♂ (USNM); iii.1943, N. R Laird 1♂ (ANIC); 2.xi.1975, Conners, 2♂ (MAGNT). Port Darwin, 5♂ (SAM). Tortilla Flats via Darwin, 3.iv.1961, C. Li, 2♂ (MAGNT). 12.33S, 131.02E, Virginia nr Darwin, 4.xii.1997, S. Gregg, 1♂ (MAGNT). 13.45S, 138.41E, Daly R Mission, 2♂, 14.i.1974, at light, J. F. Hutchinson (ANIC). QLD: 1♂ (no other locality given) (SAM). 16.49S, 145.38E, Kuranda, G. Bryant, F.P. Dodd, 1♂ (BMNH).

DIAGNOSIS. Males small (5-5.5mm long), pale brown; with large eyes which are almost contiguous ventrally and bear posterolateral excavations which are visible when head is withdrawn; antennal sockets contiguous, mouthparts small, no frontal area defined, no obvious frons-vertex junction; pronotum (Fig. 19C) subparallel-sided; elytra with interstitial lines 1, 2 well defined; epipleuron and sutural ridge evanescent in posterior half; abdominal sternite 7 broadly rounded posteriorly, lacking any defined median posterior projection; ventral surface of tergite 8 lacking ridges or flanges. Aedeagus with a very short median lobe and broad hair bearing lateral lobes. Females are not associated.

Male. Ballantyne (1968) redescribed and figured males.

DISTRIBUTION. Queensland records for this species require confirmation; modern collections have not located it. It is otherwise known only from the Northern Territory near Darwin (Fig. 23).

REMARKS. Lea (1909) considered this species resembled species of *Atyphella* except for the exposed head; there is a superficial colour similarity only. *Luciola cowleyi* is similar to *Luciola discicollis* Laporte, the 'West African Firefly', in size, colour and aedeagal form, but *L. discicollis* lacks the posterolateral excavation of the eye (Kaufmann, 1965). Ballantyne (1968) considered, but rejected, the possibility of *L. cowleyi* being a species of *Bourgeoisia* Olivier because of the eye excavation.

Luciola (Luciola) dejeani Gemminger
(Figs 19, 21)

Lampyris apicalis Boisduval, 1835: 127. *Nec* Eschscholtz, 1823: 114.
Luciola Dejeani Gemminger, 1870: 1651. Masters, 1886: 289. Olivier, 1902: 77; 1907: 51; 1910: 42.
Luciola dejeani Gemminger. Olliff, 1890: 652. Lea, 1909: 108; 1921a: 197; 1921b: 66.
Luciola (Luciola) dejeani Gemminger. McDermott, 1966: 103. Calder 1998: 179.

TYPE. Holotype. ♂ *Lampyris apicalis* Boisduval, New Holland, not located in MNHP by this author in Nov. 1993.

MATERIAL. 2 specimens. Australia: 1♂ (SAM), 1♂ (AM). (Specimens bear no labels other than 'Australia' but Olliff (1890) records one from the Northern Territory at the Victoria R Depot (15.40S, 130.39E).

DIAGNOSIS. Males 8.0-8.5mm long; the only Australian *Luciola* with a yellow dorsal surface and black elytral apices; superficially similar to *Atyphella costata* Lea in colouration, distinguished most obviously by the form of the aedeagus.

DESCRIPTION. *Male*. 8-8.5mm long; pronotum, MS, MP and elytra, except for an apical black area, yellow orange; head, antennae and mouthparts dark brown; ventral thorax yellow, legs yellow except for dark brown apices of tibiae, and dark brown tarsi; basal abdominal sternites yellow; sternite 5 yellow, with irregular brown markings in posterior 1/2; sternites 6 & 7 white; basal abdominal tergites yellow; tergites 6-8 brownish yellow.

Pronotum (Fig. 19B) 3.2mm wide; 1.7mm long; W/L 1.8; midanterior margin rounded, moderately strongly produced beyond anterolateral corners; lateral margins subparallel and narrowly explanate; midposterior margin indented or not. Elytra with 3 feebly elevated interstitial lines (1, 2 & 4).

Head slightly depressed between the eyes; GHW 2-2.1mm; SIW 0.8mm; ASD subequal to ASW. FS1 almost as long as scape, and slightly > FS2; FS 3-5 subequal, slightly shorter than 2 and slightly longer than subequal 6-8; FS 9 elongate, slender, slightly longer than 8; all FS more than twice as long as wide. Mouthparts well developed; apical segment labial palpi flattened and dentate.

Epipleuron and sutural ridge evanescent before elytral apex.

Light organs occupying sternites 6 & 7; retracted from lateral and posterior margins of sternites 6 and 7; sternite 7 with posterior margin rounded; posterolateral corners of sternite 7 not produced. Nature of ventral surface of tergite 8 not determined.

Aedeagus (Fig. 21L-N) with basal piece well developed but not hood like; ML not swollen at EO and tapering towards apex and slightly shorter than LL; LL broad, closely approximate dorsally for 3/4 their length, apices narrowed, widely separated and visible ventrally; bearing fine hairy lobes along their inner (ventral) margins.

DISTRIBUTION. Not reliably known, may not be Australian.

REMARKS. A definite Australian record of this species now rests on one specimen, apparently taken during Mitchell's Victoria R. expedition and tentatively designated by Olliff (1890) as *Luciola dejeani* Gemminger. Lea (1909) confirmed this identification and subsequently (1921b) described a further male, bearing Blackburn's name label '*Luciola dejeani* Gemming' but lacking a locality label. Lea presumed it came from Darwin. LB has re-examined both these specimens, which may be conspecific with *L. dubia* Olivier from India. Further specimens of *dejeani* have not been located and LB believes that the original specimen Olliff saw may have been mislabelled. It is absent from recent collections from MAGNT, but LB has examined four males of the similarly coloured *A. costata* from Victoria River Depot which is close to Timber Ck.

If there are two species of Australian Lampyridae with pale dorsal colouration of yellow with black tipped elytra, viz. *A. costata* (Lea) and *L. dejeani* Gemm., then a single line of Boisduval's (1835) description, viz. 'dessous jaune', becomes critical in their separation. Only the two specimens assigned here approach the description of *L. dejeani*; *costata* has at least two dark abdominal sternites and is transferred to *Atyphella*.

Lea (1921b) described the abdomen of the second male with an additional segment 'a very small white one, inconspicuously attached to the tip of the fifth, and obscured by pubescence'. There is no additional segment; he was referring to either the tip of the aedeagus or the aedeagal sheath.

Luciola (Luciola) flavicollis Macleay
(Figs 19, 20, 21, 22)

Luciola flavicollis Macleay, 1872: 263. Masters, 1886: 289. Olliff, 1890: 653. Olivier, 1902: 79; 1907: 52; 1910: 42. Lea, 1909: 109; 1921a: 197; 1921b: 65. *Nec* Armitage, 1908: 28.

Luciola (Luciola) flavicollis Macleay. McDermott, 1966: 104. Calder, 1998: 179.

Luciola Gestroi Olivier, 1885: 366; 1902: 79; 1907: 52; 1910: 42; 1913: 417 (Synonymy). Masters, 1886: 289. McDermott, 1966: 104.

Luciola gestroi Olivier, 1909b: lxxxi. Lea, 1909: 109. (Synonymy).

Luciola coarcticollis Olivier, 1888: 59; 1902: 76; 1907: 51; 1909b: lxxxi; 1910: 42. Lea, 1909: 109 (Synonymy).

Luciola flavicollis var. *coarcticollis* Olivier. McDermott, 1966: 104 (Synonymy).

Nec Luciola gestroi var. *nigra* Olivier, 1885: 366. McDermott, 1966: 104.

TYPES. Holotype. ♀ *Luciola flavicollis* Macleay S Qld: 25.37S, 151.37E, Gayndah (AM). Paratypes, *Luciola flavicollis*, 5 ♂, 2 ♀ S Qld: Wide Bay and Gayndah; Northern Territory: Port Darwin (AM, ANIC, SAM). Syntype♂ *Luciola gestroi* Olivier N Qld: Cape York (MCG).

Syntype ♂ *Luciola gestroi* var. *nigra* N Qld: Cape York, Somerset (MCG). Holotype♂ *Luciola coarcticollis* locality in Australia unknown (MNHP, Box 72 of Olivier collection).

MATERIAL. Eleven types and 285 specimens. Variability in elytral colour pattern is indicated against individual specimens as follows: Bp = base of elytra pale (Fig. 19G-J); Sd = sides of elytra dark (Fig. 19H); Bd = base of elytra dark (Fig. 19K). Unless otherwise indicated the lateral and sutural margins are at least narrowly pale. NORTHERN TERRITORY: 11.09S, 132.09E, Black Point, Coburg Pen., 15-23.ii.1977, TW, 1♂ Bd, (ANIC). 12.15S, 136.49E, Eldo, 8ml S of Gove airport, 12-16.i.1971, TW & A. Allwood, 2♂ Bp (MAGNT) 12.26S, 130.56E, Thorak Reserve via Berrimah, 28.ii.1974, ex light trap, A. Allwood, 1♂ Bp. 12.28S, 130.50 E Darwin, 14.v.1962, C. Li, 1♀Bp; A. Lea, 2♀ Bp (SAM). Lee Point, Darwin, 8.iii.1967, MU, 2♂ Bd (ANIC). Nightcliff, Darwin, 10.v.1955, L. Crawford, 1♀ Bd (MAGNT). Port Darwin, 3♂Bp 1♀Bd (SAM); 2♀Bd, 1♀ Bp (BMNH); iii.1909, 1♂ Bd (BMNH). 12.33S, 131.02E, Virginia, xi.1997-15.i 1998.S, Gregg, 8♂ Bd, 1♀Bp (MAGNT). 13.21S, 131.08E, Robin Falls, c. 12kms S of Adelaide R, MV light, 3.xii.1980, M. Malipatil, 1♂ Bd. 13.58S, 130.56E, Daly R, 'Dargie's', 7.1.1956, L. Crawford, 1♂Bp. 13.58S, 136.27E, Angurugu, 3.xii.1976, J. Waddy, 1♀ Bp. 14.28S, 132.16E, Katherine, at light, 7.ii.1968, J. Watson, 1♂, 3♀ Bp, Sd; 9.ii.1968 1♀Bp, Sd (ANIC); at light 6-10.xi.1968, E. Matthews, 5♀ Bp. Sd. 14.31S, 132.22E, Tindal, 1-20.xii.1967, light trap, W. Vestjens, 5♂, 1♀ Bp, Sd. GULF OF CARPENTARIA: 16.00S, 137.30E, Pellew group, Horn Islet, 15-21. ii. 1968, BC, 3♂, 3♀ Bp, Sd ; 1-7 . ii. 1968, 20♂. 5♀ Bp, Sd (UQ). Pellew group, South West Is., 7.ii.1968, BC, 1♂, 1♀, Bp, Sd. Groote Eylandt, Tindale, 2♂ Bd, 1♂ Bp (SAM); 21.i.1925, G Wilkins, 1♂ Bp (BMNH). QLD: Cape York Pen.: 10.48S, 142.28E, 3kms E. of Lockerbie, 30.i-4.ii.1975, GBM, RF, 1♀ Bd at MV light (QM). Lockerbie area, 13-27.iv.1973, GBM, 1♀ Bd. 10.53S, 142.24E, Bamaga, i.1969, R. Trundle, 2♂ Bd (UQ). 12.41S, 141.53E, Hibbard Point, Weipa, GBM, 3-6.ii.1976, 1♀; 5-8.ii.1975, 1♂ Bd (QM). 12.43S, 143.17E, Quinn Park, Claudie R, 12-21.ii.1985, E. Edwards, B. Hacobian, 1♂ Bp (ANIC). Claudie R nr Mt Lamond, 5-19.i.1972, DKM & G. Holloway, 2♂, 2♀ Bd (AM). 12.43S,143.18E, 11km ENE of Mt Tozer, 11-16.vii.1986, TW, A. Calder, 1♂ Bd (ANIC). 12.44S, 143.17E, Iron Ra.: 28.iv.1968-5.v.1968, GBM, 7♂, 4♀, (4♂, 1♀ Bd 2♂, 3♀ Bp); 5-10.v.1968, 4♂, 4♀, Bp; 11-17.v.1968, 11♂, 4♀ Bd; 26-31.v.1971, 2♂, 1♀ (1♂ Bp, 1♀Bd) (UQ); 1-4.v.1973, 2♂ Bd (QM); v.1966, GB, 2♂ Bd (ANIC), 14.v.1971, 2♂ Bd (MV), v.1971, 3♂, 3♀ Bd (ANIC); 13.v.1971 at light, 5♂, 1♀ Bd,100', GB (BMNH); 2♂ 1♀ Bd (SAM). 12.46S,143.17E, Claudie R, 1♂ Bd (MV); nr Mt Lamond, 5-19.i.1972, DKM, 3♂ Bd. 1♀ Bd (AM). E Claudie R, 1.vii.1982, MV light, M. Schneider, G Daniels, 1♂ Bd (UQ). W Claudie R, Iron Ra., 3-10.xii.1985, in RF, 50m, GBM, DC, 1♂ Bd (QM). 15.05S,145.20E, Gap Ck, 5km ESE of Mt Finnigan, 13-16.v.1981, A. Calder, 1 ♀ Bd (ANIC). 15.28S,141.45E, Mitchell R Mission, iii.1966, H. Standfast , 3♂ Bp, 8♂ Bd (UQ); 1.iv.1960, E. Marks, 1♂ Bp; iv.1969, A. Dyce, 2♂ Bp (ANIC). Silver Plains, JLW, 15♀, 1♂ Bd (6♀ taken 1-iv.1960 at homestead) (ANIC); 11.xii.1964, 3♂ Bp, 2 larvae (T.132, UQ). Goanna Ck, 17.ii.1964, 3♂ Bp (T.77). 15.48S,145.25E, Cooktown, i.1971, GB, 1♂ 1♀ Bd (ANIC). 16.05S, 145.29E, Cape Tribulation, 22.ix-7.x.1982, GBM, DY, GT, 1♀ Bd (QM); 24-28.xii.1981, N.Gough, R. Storey, 2♂ (DPI); Youth Hostel, 8-10.xii.1984, R.de Keyzer, 1♀ Bd (UQ). C.Tribulation area, 11.v.1992, JL, 1♂ Bd (ANIC); 21-28.iii.1984, A. Calder, TW, 2♂ Bd taken with one *L. nigra* (ANIC). Upper Daintree R, 27.xii.1964, GBM, 1♂Bd (UQ). Cow Bay, N of Daintree, 18-25.i.1984, I. Cunningham, 1♂ (DPI). 16.49S,145.38E, Kuranda, 1500', 9.x.1951, J. Sedlacek, 1♀ Bd (UQ). 16.53S,145.42E, Redlynch, R. Tillyard, 1♂, 1♀ Bd (MV); 4.xii.1939, R. Wind, 13♂ Bd (BMNH). 16.55S,145.46E, Cairns, A. Lea, 16♂Bd, 2♀Bd (4 attracted to light; AM; SAM); GB, ii.1950, 3♂ Bd (ANIC), xii.1950, 2♂, 1♀ Bd; 6♂, 4♀Bd (MV); 3♂, 2♀ Bd (BMNH);7♂, 3♀ Bd (ANIC); 16.iv.1960, K. Harley, 2♂ Bd. 17.08S, 145.13E, Mutchilba, ii.1933, A. Selby, 3♂ Bp (MV). 17.34S, 145.55E, Coorumba, R. Mulder, 27-28.v.1983,1♂, 5♀ Bd (AM). 18.39S,146.10E, Ingham, 4.ii.1961, I. Cook, 2♂ Bd (UQ); 8.ii.1972 N. McFarland, 2♂, 1♀ Bd (ANIC). 19.30S, 146.58E, Mt Elliot NP 9-10.ii.1990, K. Dunn, T.

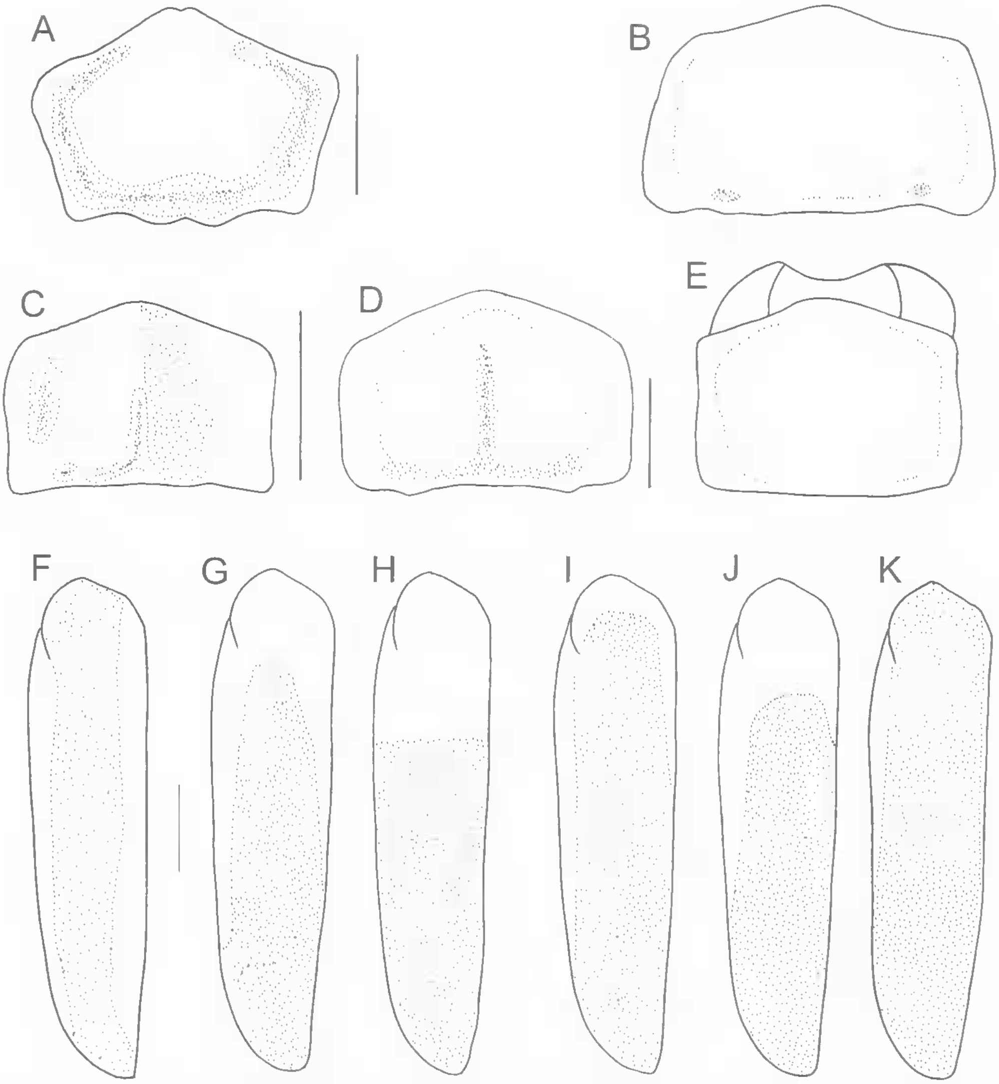

FIG. 19. *Luciola* spp. A-E, dorsal view of pronota; F-K, dorsal view, left elytron. A, G-K, *L. flavicollis*; B, *L dejeani*; C, *L cowleyi* (left side indicates sculpturing, right side colour pattern); D, *L. nigra*;E, F, *L orapallida* (E with anterior margin of head). Elytral colour patterns described in text as Bp (G-J); Sd (H); Bd (K). Scale lines 1mm; lines shared by A, B; C, E; G-K are not to scale.

Woodger, 1♂ Bd. 19.34S,147.24E, Ayr, i. 1961, I. Bayly, 1♀ Bp (UQ). 20.15S,148.23E, Greta Ck, 20mi. N of Proserpine, 1.i.1965, GBM, 1♂, 1♀Bp (QM); 1.i.1965, H. Rose, 2♂ (1 Bp1 Bd) (UQ). 21.09S, 149.11E, Mackay, ii.1964, E. Dunwoody, 1♂. 21.18S, 149.18E, Halftide, nr Mackay, 8.ii.1965, to light, E. Dahms 1♂ Bp (QM). 23.08S, 150.22E, Yaamba, attracted to light, 4-5.i.1962, LP, 1♂ Bd, 9.1.1962, 1♂Bp (UQ). 23.11S,150.73E, Yeppoon, 25.i.1975, H. & A. Howden, 2♂ Bp (ANIC). 23.22S, 150.32E, Caves (probably Olsen's Caves) nr Rockhampton, R. Higgins, 3♀, 2♂ Bp (QM). 24.53S, 147.40E, Carnarvon, 31.i.1962, E. Exley, 1♂ Bp (UQ). 26.03S, 152.24E, Woolooga, 20.viii.1965, R. Drew, 1♂ Bd.

DIAGNOSIS. Males small (4.5-6.5mm long); pronotum orange; elytra light or dark brown, always with some paler yellow or orange markings along sides or across base; ventral body very dark brown to black except for pale yellow prothorax, yellow areas of legs, and white light

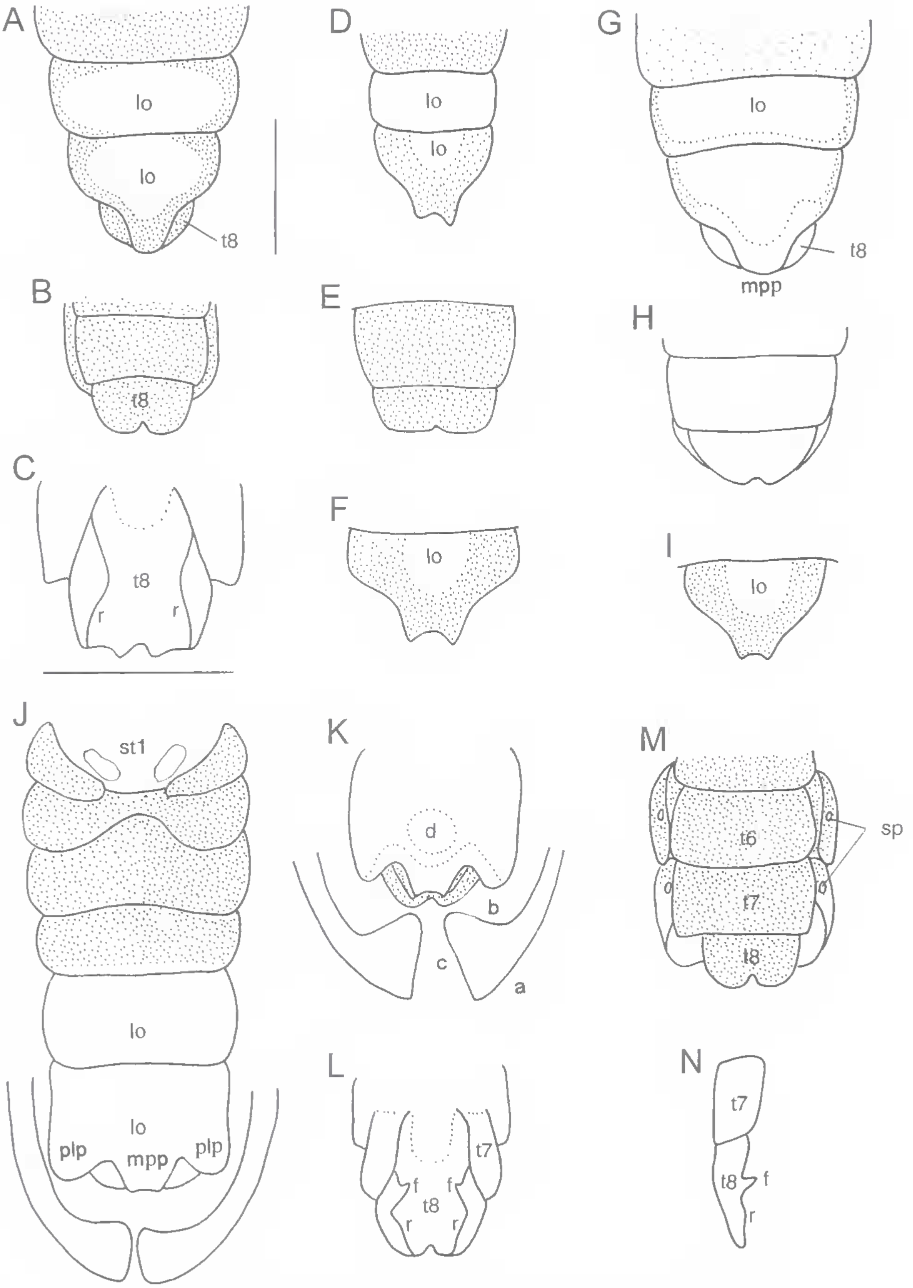

FIG. 20. A-I, Terminal abdomens of *Luciola* spp. A,D,G,F,I, ventral aspect terminal sternites; B,E,H dorsal aspect terminal tergites; C, ventral aspect terminal tergites. A-C, *Luciola nigra*; D-F, I, *L. flavicollis*; G, H, *L. orapallida*. J-N,Terminal abdomens of *Pteroptyx* spp. J,K, entire abdomen (J) or sternite 7 only (K) with deflexed elytral apices; M, dorsal aspect terminal tergites; L, N, ventral (L) and right lateral (N) aspects of terminal tergites. J, L-N, *P. platygaster*; K, *P. cribellata*. Scale lines 1mm; lines shared by A-B, D-N; C. a-c = dimensions of deflexed elytral apex; d = dimple; f = flange; lo = light organ; mpp = median posterior projection sternite 7; plp = posterolateral projection sternite 7; r = ridge; st 1 = sternite (ventrite) 1; t7,8 = tergites 7, 8.

organ; any posterolateral excavation of eyes hidden when head is withdrawn into pronotum; MPP of sternite 7 prolonged, sub-parallel-sided and apically emarginate; posterolateral corners of sternite 7 defined and rounded. Female macropterous, coloured as for male except pale light organ in sternite 6 only.

DESCRIPTION. Females are redescribed; males and larvae are newly described.

Male. 4.5-6.5mm long; pronotum, MS and MN orange; elytra (Fig. 19G-K) moderately light to quite dark brown, with suture and lateral margins yellow at least in basal 1/4; (specimens from Olsen's Caves have yellow elytra with pale brown markings); base of elytra either light to quite dark brown, or orange yellow in basal 1/6-1/3); variability in elytral colour pattern is indicated above; males from same locality showed such variability; head black, antennae black or reddish orange; ventral prothorax orange, meso and metathorax dark brown to black, occasionally orange; legs 1 dark brown to black except for orange coxae, trochanters and most of femora; legs 2 and 3 black except for orange coxae, trochanters and base of femora; ventral abdomen dark brown or black except for white sternite 6 (lateral margins of which may be dark if light organ does not reach lateral margin), and white light organ in the anterior half of 7; all abdominal tergites black.

Pronotum 1.2-1.8mm wide; 1.0-1.3mm long; W/L typical male 1.4; midanterior margin considerably produced beyond anterolateral corners; lateral margins sub-parallel or converging posteriorly; depressed areas as figured (Fig. 19A); punctures contiguous over most of disc. Head deeply depressed between eyes; GHW 1.1-1.5mm; SIW 0.3-0.4mm; ASD subequal to ASW. FS 1 slightly longer than remaining subequal FS.

Elytral epipleuron and sutural ridge evanescent before elytral apex.

Light organs occupying sternite 6 entirely and sternite 7 in median anterior half or less (Fig. 20D-F,I); MPP of sternite 7 well developed, sub-parallel sided, apically emarginate, sometimes slightly asymmetrical at apex. Ventral surface of tergite 8 with lateral ridges, lacking flanges. Aedeagus (Fig. 21U-W) with ML slightly swollen at apex, and bearing a median dorsal ridge which is irregularly serrated; LL broad at their apices, which bear incurving hooks on the ventral surface of their inner apical angles.

Female. 5.4-6.0mm long (holotype 6.0mm). Macropterous. Coloured as for male except white light organ confined to sternite 6, and sternites 7 & 8 black. Holotype female dorsal colour pattern is Bd; females show same variability in dorsal colour pattern as males. Pronotal outline similar to that of male. Median posterior margin of sternite 8 broadly and shallowly emarginate, of 9 entire.

Larva. Presumed *flavicollis* larvae differ only from larvae of *L. nigra* in lacking the pronounced marginal tubercles in the anterior half of tergum 1 and in having deep grooves in the posterior 1/4 of the protergum.

DISTRIBUTION. New Guinea (Olivier 1913), northern Australia and Gulf of Carpentaria islands, and south along the east coast of Queensland to Woolooga near Gympie. Often from open forest where it may be attracted to light; not known from rainforest (Fig. 24). Olivier (1913) recorded *L. gestroi* from New Guinea.

REMARKS. Macleay (1872) confused the sexes, and consequently described the terminal abdomen inaccurately. Olliff (1890) described as luminous the penultimate segment of the female (only the antepenultimate, sternite 7, bears the light organ). Lea (1921b) correctly described the female abdomen but incorrectly attributed a medio-basal white patch to the 'subapical' abdominal segment of the male (the light organ is reduced to a 'sub-apical patch' as he described on the terminal abdominal sternite only). Lea (1909) indicated the Victoria record for *L. coarcticollis* was erroneous, and recorded the species from northwestern Australia, Northern Territory and South Australia. The South Australian record is also false. LB has been unable to relocate all these specimens.

Armitage (1908) described the 'Queensland firefly beetle' with entirely dark elytra and misidentified it as *L. flavicollis*. His specimens were either *L. nigra* or a *Pteroptyx* sp.

Dorsal colour patterns vary, often between males and/or females from the one site. The BpSd colour pattern is restricted to Katherine and the Pellew Islands group.

Luciola (Luciola) nigra Olivier
(Figs 19, 20, 21, 22, 36D)

Luciola Gestroi var. *nigra* Olivier, 1885: 366.

Luciola (Luciola) nigra Olivier stat. nov. Ballantyne in Calder, 1998: 179.

Luciola humilis Olivier, 1896: 2; 1902: 80; 1907: 52. Lea. 1909: 108; 1921a: 7. Ballantyne in Calder, 1998: 179.

Luciola (Luciola) humilis Olivier. McDermott, 1966: 105. Ballantyne in Calder, 1998: 179 (synonymy).

Luciola scutellaris Lea, 1929: 344. Ballantyne in Calder, 1998: 179 (synonymy).

Luciola (Luciola) scutellaris Lea. McDermott, 1966: 113.

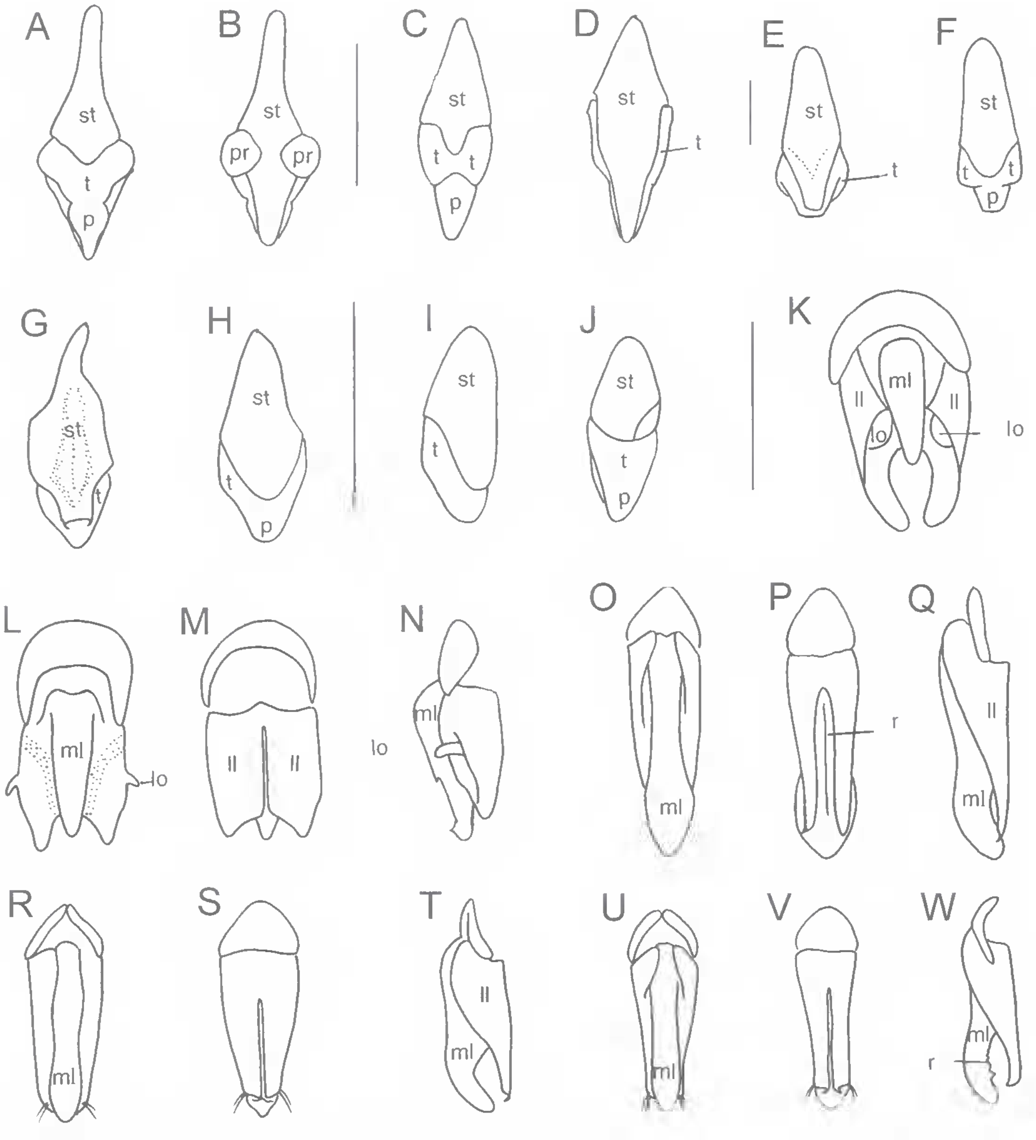

FIG 21. Aedeagal sheaths and aedeagi of *Luciola*, *Pteroptyx* and *Atyphella* spp. A-J, aedeagal sheaths, dorsal (A, C, F, H, J), ventral (B, D, G, I). K-W, aedeagi, ventral (K, L, O, R, U), dorsal (M, P,S, V) and left lateral (N, Q, T, W). A-D, *Pteroptyx* sp.; E, F, O-Q, *L. orapallida*; G, H, K, *L. cowleyi*; I, J, *Atyphella* sp.; L-N, *L. dejeani*; R-T, *L. nigra*; U-W, *L. flavicollis*. Scale lines 1mm; lines shared by: A-D; I, J; L-W. ll = lateral lobe; lo = fleshy lobe of lateral lobe; ml = median lobe; p = protiger; pr = paraprocts; r = ridge; st = sternite 9 of aedeagal sheath; t = tergite 9 of aedeagal sheath.

TYPES. Holotype. ♂, *Luciola humilis* N Qld: Cairns (BMNH). Paratypes, 4♂ 4♀ *Luciola scutellaris* Northern Territory: Gulf of Carpentaria: 13.09-14.06S, 136.28-136.38E, Groote Eylandt , N. Tindale (117051, SAM; QM). Paratype♂ *Luciola gestroi* var. *nigra*: N Qld, Cape York, Somerset Is. (MCG).

MATERIAL. 7 types and 432 specimens. Specimens with mesoscutellum black are indicated thus: #. NORTHERN TERRITORY: 11.01S, 136.45E, Rimbija Is, Wessell Islands, 21.i.1977, E. Edwards, 1♂ # (ANIC). 11.07S, 132.08E, Smith Point, Cobourg (sic) Pen., 5-6.ii.1977, R. Lewis, 1♂; 26.i.1977, E. Edwards, 1♂ #. 11.09S, 132.09E, Black Point, Coburg Pen., 15-23.ii.1977, TW, 1♂, 1♀ #; 24.i.1977, E. Edwards, 1♀. Lee Point, Darwin, 7-8.iii.1967, 1♀, 1♂, 6♂ #; 4 mi. S of Lee Point, 6.iii.1967, MU, 1♂ # . 12.52S, 132.50E, Kakadu NP, Nourlangie Camp, 17-18.xi.1979, MV light, M. Malipatil, 1♂ # (MAGNT). 13.33S, 131.13E, Green Ant Ck, 40 ml S Adelaide R, 25.i.1971, TW, A. Allwood, 2♂, 1♀. NW AUSTRALIA: 2♂ (ANIC). TORRES STRAIT: Murray Is., 10m, 26.ii.1984, J Sedlacek, 1♀ # (QM). QLD: 12.44S, 143.15E, Claudie R, xi.1912-ii.1913, J. Kershaw, 4♂ (ANIC). 13.57S, 143.12E, Coen, Cape York Pen., 4mi. N on road to aerodrome, 21.xii.1964, LP, 3♂, 7♀(T.146, UQ). Mt White, via Coen, 21.xii.1964, LP, 2♂, 1♀ (T.145). Breakfast Ck, Silver Plains, Cape York Pen., 11.xii.1964, JLW, 1♀, 1 larva (T.141); 12.xii.1964, LP, pr in cop, # (T.128). 14.07S, 142.32E, Stewart R, 1-ii.1927, Hale, Tindale, 1♂# (SAM). 15.50S, 145.20E, Gap Ck, 5km ESE of Mt. Finnigan, 13-16.v.1981, A. Calder, 2♂, 1♀(ANIC). 16.05S, 145.29E, Cape Tribulation, at Youth Hostel, 8-10.xii.1984, R. de Keyzer, 1♂ (UQ). Cape Tribulation area, 1-11.v.1992, JL, 2♂ # (ANIC). 16.08S, 145.17E, Cooper Ck, 13mi. N of Daintree R., 29-31.xii.1972, BC, 2♂, 3♀ (UQ). 16.28S, 145.23E, Mossman Gorge, 320ft, at light, 31.x.1966, EB, 1♂ (ANIC). Mossman Gorge, via Mossman, 25-26.xii.1964, GBM, 2♂, 1♀ (UQ), 1♂ (T.134 UQ). 3mi. W of Mossman, iii.1964, IC & MU, 1♂ (ANIC). 16.41S, 145.20E, Bakers Blue Mts., 17km W of Mt. Molloy, 30.xii.1989-9.i.1990. ANZSES Exped., 800-1000 m, 18♂ (1♂ #), 5 E (1♀ #) (QM). 16.45S, 145.36E, Black Mt Rd, 11.4 road kms from Kennedy Hwy; 8km NNW of Kuranda, Stop A-27, 26.ii.1988, D. Rentz, 1♂ # (ANIC). 16.49S, 145.38E, Kuranda, 20.i.1919, F. P. Dodd, 2♂, 1♀ (UQ); 28.xii.1963, GBM, 3♂ (T.19); 2.iii.1908, R. Armitage, 4♂, 3♀ (3♂, 2♀#: MV); 4♂, 4♀ (SAM); ii.1914, F. Dodd, 2♂, 3♀ (1♂, 2♀ # ; SAM). Barron Falls, 2.i.1965, GB, 1♂ (ANIC). 16.49S 145.11E, Hann Tbld (N end), 11-14.xii.1995, RF, 950-1000m, GBM, GT, 1 larva (QM). 16.53S, 145.42E, Redlynch, R Wind, 21.x.1983 1♂, 1♀ #; 4.xii.1983 5♂(1♂ #), 2♀ (1♀ #); xii.1938, R. Sternitzky, 1♂, 7♀ (BMNH). 16.54S, 145.44E, Edge Hill, xii. 1966, GB, 3♂ (ANIC). 16.55S, 145.15E, Hann Tbld Radar Station, 950m, 26-27.xi.1998, CB, 1♂ (QM). 16.55S, 145.40E, Mt Williams summit, 1000m, 27.xi.1997–6.ii.1998, RF FIT, GBM & DC, 1♂. 16.55S, 145.46E, Cairns: E. Allen, 1♂#, 1♂, 1♀, 2♀ # (ANIC; MV); H. Carter, 1♂, 1♂ #, 1♀(MV); x.1921, A. Lea, 1♂(MV); A. Lea, 2♂, 4♀ (1♀#; SAM); 21.xii.1981, T. Hawkeswood, at light, 1♂ (ANIC); 3♂ (1♂ #), 2♀ # (MV); 23.xi.1934 2♂ # (ANIC); 4♂(1♂#), 4♀ (MM, SAM); 5♂ (3 #), 4♀(2 #) (BMNH). Crystal Cascades, via Cairns: 9.xii.1964, LP, 4♀, 16♂ (UQ), 2♂, 2 larvae (T.148); 29.xii.1963, GBM, 1♂, 3♀(T. 9, 10). 17.05S, 145.47E, Gordonvale, 1930, E. Allen, 1♂ #, 1♂, 1♀ (QM). 17.05S, 145.46E, Meringa, 1♂(MV). 17.16S, 145.29E, Atherton, 30.i.1960, G. Ettershank, 1♂ (UQ); ii.1975, H. Howden, 9♂, 1♀ (2♂, 1♀ #) (OTT). 17.10S, 145.33E, Kauri Ck, Tinaroo Dam, 24.iv.1970, GBM, 1♂ # (UQ). 17.12S, 145.51E, Bellenden Ker Ra., Cableway Base Stn., 100m, 17.x-9.xi.1981, Earthwatch/Qld Museum, RF, 1♂, 3♀ at MV light, 1♂, beating (ANIC). 17.16S, 145.29E, Tolga scrub, via Atherton, 28.xi.1964, R. Elder, 2♂, 1♀ (T.205 UQ). 17.17S, 145.37E, Lake Eacham, 6.i.1964, GBM, 1♂ (T.8). 17.20S, 145.25E, Baldy Mt Rd, 2.7km from S end, 30.xi.1997-5.ii.1998, 1160m, open forest intercept, GBM & DC, 1♀ (QM). 17.21S, 145.56E, Boulders, via Babinda, 15.xii.1966, BC, 1♂ (T.213, UQ). 17.28S, 146.01E, Stone Ck via Garradunga, 14-19.iv.1997, GBM, CB, 2♂ (QM); 15-18.iv.1997, 100m, GBM, Russell, Ovenden, 1♂, 1♀ (QM). 17.31S, 145.37E, Millaa Millaa Falls, 10-11.xii.1966, BC, 24♂, 7♀ (UQ), 2♂ (QM); 5.xii.1965, GBM, 2♂, 1♀ (T.198 UQ). 17.32S, 146.01E, Innisfail, i.1964, J. Gilchrist, 1♂ (taken with *P. cribellata* and *L. flavicollis*) (T.84, UQ); 25.v.1961, G. Shaw, 1♂. 17.33S, 145.31E, Chilverton, 22.xii.1964, H. Rose, 9♂, 6♀ (T.150 UQ). 17.34S, 145.55E, Coorumba, R. Mulder. 18.11.1975, 1♂; 26.iii.1977, 1♂; 28.v.1983, 4♂, 1♀ (AM). 17.36S, 145.45E, Henrietta Ck, 6.xii.1965, GBM, 10♀ (T.187 UQ). 17.36S, 145.29E, Ravenshoe, 23.xii.1964, H. Rose, 1♂; 28.xii.1964, GBM, 7♂. 17.54S, 145.39E, Tully R causeway, 750m, 2.xii.1998, GBM, DC, P. Bouchard, 1♂ (QM). 18.22S, 146.15E, Hinchinbrook Is., Black Sands Beach, 21.i.1987, SH, 3♂ (2♂ #). 19.03S, 146.24E, 2mi. ENE of Rollingstone, 26.iv.1969, IC, MU, 1♂ # (ANIC). 20.24S, 148.34E, Greta Ck, 20mi. N of Proserpine, 1.i.1965, GBM, 1♂ (UQ). 21.09S, 148.38E, Finch Hatton Gorge, 19.iv.1968, GBM 1♂ #. 24.12S, 151.47E, Eurimbula Ck, via Round Hill Head, 15.xii.1976, GBM, SRM, 6♂. 25.26S, 152.08E, Mt Goonaneman, via Childers, 6-7.ii.1981, GBM, 1♂ (QM). 25.30S, 151.50E, Bin Bin Ra., 19.xii.1974, H. Frauca, sweeping, 2♂ (ANIC). 25.31S, 152.03E, 10mi. W of Biggenden, 7.i.1972, H. Frauca, 1♂. 26.28S, 152.41E, Imbil, 25.i.1936, F. A. Perkins, 3♂, 3♀ (UQ). 26.38S, 152.58E, Nambour, 14.i.1962, (in house at night), H. Greening, 1♂. 26.42S, 152.54E, Montville, Deane, 1♂, 1♀. 26.46S, 152.51E, Maleny, i.1928, HH, 8♂ (QM, SAM). 27.22S, 152.53E, Samford, 28. ii. 1960, J. Bryan, 1♂ (UQ). 27.28S, 153.02E, Brisbane, 24.ii.1925, HH, 1♂, 2♀ (QM), 3.i.1962, T. Brooks, 1♂ (UQ), 11.i.1965, E. Tay, 1♂, 5.i.1962, K. Barnard, 1♂. Brisbane, UQ Mine site at Indooroopilly, 13.ii.1962, LP, 1♀ (T.71). Brisbane suburbs: (Alderley), 23.i.1957, W. Treloar, 2♂ (QM); (Chelmer), 15.iii.1942, H. Longman, 1♂ (QM); (Indooroopilly), 24.i.1973, T. Lambkin, 1♂. Petrie, 3.ii.1962, J. Akers, 1♂ (T.72, UQ). 27.34S, 153.08E, Tamborine, i.1961, P. Webb, 1♂ (T.69). 27.34S, 151.57E, Toowoomba, 7.i.1964, J. Cardale, 1♂. 28.05S, 153.27E, Burleigh Heads NP, xii.1963, LP, 2 larvae (T.43).

DIAGNOSIS. Males small to medium (4.8-7.6mm long); pronotum orange, MS orange or black; elytra very dark brown, almost black; ventral surface of metathorax, and of abdominal sternites 2-5 black; white light organ (Fig. 20A) occupying all of sternite 6 (lateral margins sometimes dark brown); light organ restricted to median basal area of sternite 7, which is otherwise black; pronotal punctures small, shallow, mostly contiguous; MPP of sternite 7 conspicuously produced, and may be slightly emarginate at apex;

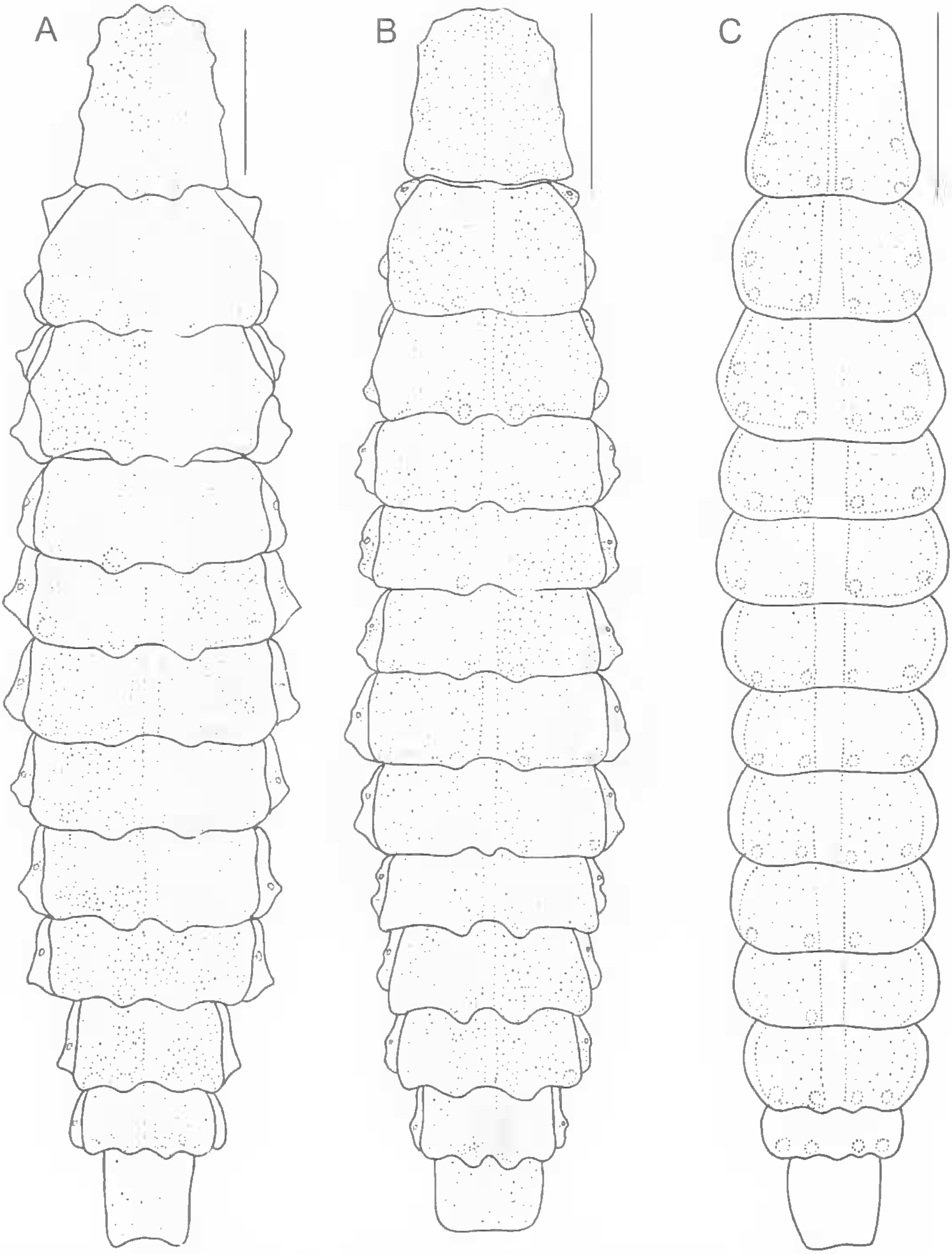

FIG. 22. Larvae of *Luciola* spp., dorsal view. A, *Luciola australis*; B, *L. orapallida*; C, *L. nigra*. Scale lines 1mm.

ventral surface of tergite 8 with lateral ridges but lacking flanges. Female macropterous, coloured as for male except for pale cream light organ in sternite 6. Larva dorsally pale with a broad pale median band.

DESCRIPTION. Males are redescribed; females and larvae are newly described.

Male. 4.8-7.6mm long; pronotum and MN orange yellow, MS orange yellow or black (variability indicated above), elytra black; head, antennae and palpi very dark brown, labrum sometimes paler brown; ventral pro and mesothorax yellow, metathorax dark brown; coxae, trochanters and basal 2/3 of femora of legs 1, 2 yellow orange, remainder dark brown; legs 3 dark brown except for pale trochanters and sometimes pale bases of femora; abdominal sternites 2-5 very dark brown, sternite 6 creamy white, sometimes with narrow dark lateral margins; sternite 7 dark brown except for median basal light organ; all tergites dark brown.

Pronotum 1.2-2.1mm wide, 0.8-1.5mm long; midanterior margin rounded, projecting conspicuously beyond anterolateral angles; lateral margins sub-parallel, or converging slightly posteriorly; punctures small, shallow, mostly contiguous; depressed areas as figured (Fig. 19D).

Elytral epipleuron and sutural ridge evanescent before elytral apex.

Head deeply depressed between the eyes, GHW 1.2-1.8mm; SIW 0.2-0.4mm; ASD < ASW. Antennal flagellar segments 1, 2 subequal, 3 slightly < 2 or 4, 5-9 subequal.

Light organs (Fig. 20A-C) occupying sternite 6 completely except sometimes for a narrow lateral margin, and sternite 7 in median basal area only; MPP of sternite 7 broadly produced, sub-parallel-sided and apically truncate, sometimes slightly emarginate; ventral surface of tergite 8 with lateral ridges and no flanges. Aedeagus (Fig. 21R-T) with basal piece narrow; LL tapering apically, bearing incurving hooks on the ventral surface of their inner apical angles; ML slightly swollen at apex, lacking a median dorsal ridge.

Female. 5.0-7.5mm long; macropterous; coloured as for male except for white light organ in sternite 7, and black sternites 8, 9; small median basal white area, presumed to be fat body, on sternite 8 on females from Crystal Cascades and Coen.

Pronotal lateral margins converging a little both anteriorly and posteriorly, or converging only in posterior 1/3. Median posterior margin of sternite 8 broadly and shallowly indented, of 9 entire.

Larva. (Fig. 22C). Larvae reliably associated. Dorsally brown (often very pale brown), with a broad median pale cream band extending from anterior margin of protergum to posterior margin of antepenultimate tergum; lateral margins of all terga except 1 widely pale; terminal 2 terga pale; venter cream, legs very pale brown.

All terga bearing well defined rounded protuberances (Fig. 22C).

DISTRIBUTION. Widely distributed, often in sclerophyll forest, across Northern Australia and down the east coast of Queensland to Burleigh Heads NP. All records south of Rockhampton have a yellow mesoscutellum (Fig. 25). Ballantyne (1992) recorded this species from New Guinea.

REMARKS. Lea (1929) doubted that *L. scutellaris* was 'other than a variety of *L. humilis* Olivier', because it differed only in having a black mesoscutellum and in the smaller size. While I have found no specimens having black mesoscutellum to approach 7.0mm long (the average length of specimens of *L. nigra*), many smaller specimens (c. 4-5mm) have an orange mesoscutellum. The variability of these features is indicated above; specimens with dark mesoscutellum occur in Queensland from Coen in the north to Rockhampton in the south. Males and females taken together often vary in the colour. A living specimen is shown in Fig. 36D.

L. nigra adults have been found in Brisbane in areas of rainforest or relict rainforest where there is much lantana (e.g. the species was in abundance in the 1960s at the University Mine site at Indooroopilly, and in suburban back yards in the Indooroopilly and St Lucia area). It was collected with *Atyphella scintillans* at the University Mine site, and at Burleigh NP (Powell, 1964), and is frequently taken with *L. flavicollis* (pers. obs.). Armitage's (1908) reference to the 'Queensland firefly beetle' was probably to this species.

Luciola (Luciola) orapallida Ballantyne sp. nov. (Figs 19, 20, 21, 22)

TYPES. Holotype. ♂ N Qld: 13.57S, 143.12E, Cape York Pen., E coast, Silver Plains: Massey R, 12.xii.1964, salt-water couch, LP (QMT62935). Paratypes: same data, 2♂, 4♀, LP,GBM&JLW (UQ, T.126). Breakfast Ck, in mangroves, 13.xii.1964, JLW, 2♀, 1 larva (T.127). Stewart R, 16.viii.1963, JLW, 5♀. TORRES STRAIT: Saibai I., 10-13.vii.1975, H. Heatwole, 1♀ (AM).

DIAGNOSIS. Male 6.0-7.2mm long; similar to *L. australis F.* and *L. flavicollis* Macleay, distinguished by the broad pale lateral bands on the elytra, the pale colour of the venter and the outline of sternite 7, and the narrow, widely separated aedeagal lateral lobes. Female macropterous, coloured as for male. Presumed larva similar to that of *L. australis*.

DESCRIPTION. *Male*. 6.0-7.2mm long; pronotum, MS and MN orange, elytra brown with wide yellow lateral and sutural margins (Fig. 19F); head, antennae and palpi dark brown; ventral surface of thorax orange; legs yellow except for dark brown tibiae and tarsi: basal 2 abdominal sternites yellow; sternites 3, 4 brown; white light organ in sternites 6 and 7; lateral margins of sternites 6 and 7 narrowly brown, posterior margin of sternite 7 narrowly yellow; all tergites yellow.

Pronotum (Fig. 19E) 1.4-2.1mm wide, 1.1-1.4mm long; midanterior margin rounded, projecting moderately beyond anterolateral angles; lateral margins subparallel or slightly convergent posteriorly; punctures relatively broad, shallow, most separated by their width, few contiguous.

Head deeply depressed between eyes; GHW 1.2mm; SIW 0.3mm; ASD = ASW; FS elongate, subequal.

Light organs (Fig. 20G,H) retracted to anterior half of sternite 7; posterolateral corners of sternite 7 rounded; MPP moderately produced, apically truncate. Ventral surface of tergite 8 with lateral ridges, lacking flanges. Aedeagus (Figs 21O-Q) with narrow basal piece; ML expanded at apex, with median dorsal ridge not serrated; LL widely separated and slightly divergent at their very narrow apices.

Female. 7.2-8.5mm long; macropterous but terminal 2 abdominal segments may protrude beyond elytral apices; coloured as for male except white light organ in sternite 6 and yellow sternites 7 and 8. Pronotum with median anterior margin rounded, barely projecting beyond anterolateral corners; lateral margins converging anteriorly slightly in anterior 2/3, converging slightly posteriorly in posterior 1/3. Head barely depressed between eyes, which are widely separated; mouthparts well developed. Median posterior margins of sternites 8 and 9 not indented.

Larva. (Fig. 22B). Associated by label data only; moderately dark brown on dorsal surface except for pale median line extending from anterior margin of tergum 1 to posterior margin of penultimate tergum; venter of body pale except for brown markings on penultimate segment, and brown terminal segment; legs brown.

Protergum with well-defined protuberances; meso and metaterga with paired midlateral, posterolateral and posterior protuberances; abdominal terga 3-11 with paired posterolateral and posterior protuberances. Distinguished from *L. australis* F. by the absence of well defined protuberances on the anterior margin of the pronotum and the uniformly brown terminal 2 terga.

DISTRIBUTION. Known only from these records in salt water couch on the coastal plain of Cape York Pen. near Coen and on Saibai I. off the S coast of New Guinea (Fig. 23).

REMARKS. The specific name (Latin, *ora* = edge, border; *pallidus* = pale, wan) refers to the pale elytral margins. This new species is superficially similar to *L. flavicollis*. It is presently known from mangrove swamps in Cape York and Torres Strait, while *L. australis* F. is known from mangroves from Gladstone to Cape Pallarenda, just north of Townsville. ‘These beetles were found only on damp drift wood, which collects and is left by very high tides during part of every year, mainly towards the end of the dry season. It usually builds up in back washes and bare patches of ground or mud in amongst the 'marine couch'. Driftwood all swept out to sea by high tides during wet season when rivers are in flood. Beetles very quiet and could be picked off debris by hand’ (J.L.H. Wassell, pers. comm.).

Pteroptyx s. str. Olivier
(Figs 20, 21)

Pteroptyx Olivier, 1902: 72; 1907: 55; 1909a: 319; 1909b: lxxxii; 1910: 47; 1911b: 16; 1913: 417. Olivier & Pic, 1909: 139. McDermott, 1964: 46; 1966: 117. McDermott & Buck, 1959: 10. Ballantyne & McLean, 1970: 223. Ballantyne, 1987a: 117; 1987b: 171. Calder, 1998: 179.

TYPE SPECIES. Olivier (1902) described *Pteroptyx* from two species, viz. *Luciola testacea* Mots. and *L. malaccae* Gorham, which were characterised by the deflexed elytral apices and the trilobed abdominal sternite 7 in the male. Lucas (1920) designated *L. testacea* as the type species of *Pteroptyx*. Ballantyne & McLean (1970) showed that since *L. testacea* lacked deflexed elytral apices, its taxonomic position is uncertain. It was Olivier's clear intention to erect a genus based on the possession of deflexed elytral apices in the male and all evidence suggests that he never saw Motschulsky's type specimen. Ballantyne & McLean (1970) considered that *L. malaccae* should be proposed to the International Commission for Zoological Nomenclature as the type species, but this has not yet occurred (Calder, 1998).

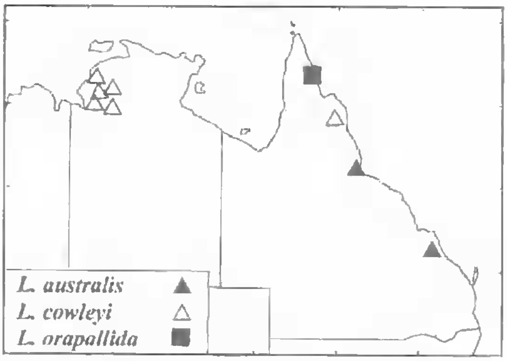

FIG. 23. Records for three species of *Luciola* in northern Australia.

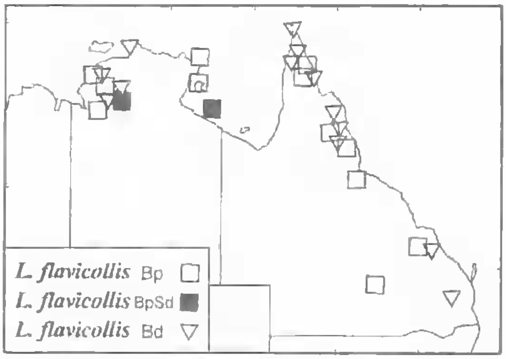

FIG. 24. Records for *Luciola flavicollis* in northern Australia, indicating distribution of elytral colour patterns.

REMARKS. The phylogenetic analysis that follows identifies a *Luciola/Pteroptyx* clade, which clearly distinguishes two Australian species of bent winged fireflies.

KEY TO SPECIES OF *PTEROPTYX* MALES FROM AUSTRALIA

1. Deflexed elytral apex with sides A, B and C subequal (Fig. 20K) . . . . *cribellata* Olivier
   Deflexed elytral apex with sides A and B much longer than C (Fig. 20J) . . . . *platygaster* (Lea)

Pteroptyx cribellata Olivier
(Fig. 20)

Luciola cribellata Olivier, 1892: 1010.
Pteroptyx cribellata Olivier, 1909a: 319. Ballantyne, 1987a: 133. McDermott, 1966: 117 (partim). Ballantyne & McLean, 1970, 242 (partim). Lloyd, 1973a: 991; 1973b: 268; 1979b: 25. Calder, 1998: 179. *Nec* Hanson et al., 1971: 161; Hanson, 1978: 2158; Haneda, 1966: 6; Buck et al, 1981a: 277, 1981b: 287.
Pteroptyx cribellatum Olivier, 1910: 47; 1913: 417. Ballantyne & McLean, 1970: 242 (synonymy).
Pteroptyx cribratellum Pic, 1932: 88. Ballantyne & McLean, 1970: 243 (synonymy).
Nec *Luciola platygaster* Lea. Olivier, 1913: 417 (synonymy). Ballantyne & McLean, 1970: 243.

TYPE. Lectotype. ♂ Papua New Guinea, Ighibirei designated by Ballantyne (1987a) (MCG).

MATERIAL. 5 specimens. QLD: Cape York Pen.: Dividing Ra., 15km W of Captain Billy Ck, 5-12. ii. 1976, GBM, 3 ♂ (synchronous flashing) (QM). 12.44S, 143.17E, Iron Ra., Gordon's Ck, 8.viii.1983, B. Gillies, 1 ♂ (MV). 26.33S, 154.05E, Coolum, 20.iv.1938, 1 ♂ (UQ).

DIAGNOSIS. Orange pronotum, dark brown elytra, tip of deflexed elytral apices truncate; distinguished from other similar species by the dimensions of the deflexed elytral apex (Fig 20K; a, b, c are subequal) and the deep depression in the median area of sternite 7 anterior to the MPP of that sternite (Fig. 20M).

DISTRIBUTION. Specimens listed here extend the range of *cribellata*. The single specimen labelled from Coolum in S Qld is erroneous and requires confirmation.

REMARKS. Olivier (1913) synonymised *Luciola platygaster* Lea with *Pteroptyx cribellata* (Olivier). However they differ by the nature of the deflexed elytral apex.

Pteroptyx platygaster (Lea) comb. nov.
(Fig 20)

Luciola platygaster Lea, 1909: 110. Olivier, 1910: 45.
Nec Pteroptyx cribellata Olivier. Olivier, 1913: 417 (synonymy). McDermott, 1966: 117. Ballantyne & McLean, 1970: 242. Ballantyne, 1987a: 133. Calder, 1998: 180.

TYPES. Calder 1998 interpreted Ballantyne & McLean's (1970) reference to a holotype for this species as a lectotype designation. This designation is confirmed. Lectotype ♂ N Qld: Cairns (SAM). A single ♂ labelled 'Cairns', mounted on a card point with abdomen and aedeagus on separate card point beneath. Paralectotypes, 1♂, 4 ♀ (SAM), 1♂, 1♀ (ANIC, MUMA) designated by Calder (1998) and confirmed here.

MATERIAL. Lectotype, 7 paralectotypes and 87 specimens. N QLD: 12.43S, 143.16E, Middle Claudie R, Iron Ra., 6.x.1974, M. Moulds, 3♀ (AM). 12.43S, 145.38E, Kuranda, F.P. Dodd, 6♂, 4♀ (UQ, SAM). 16.19S, 145.23E, Bamboo Ck nr Miallo, N Mossman, 25.iv.1967, D. Colless, ♂ (ANIC). 16.28S, 145.23E, Mossman, 25.iii.1967, MU, ♂. Mossman Gorge, 300 feet, at light, 31.x.1966, EB, ♂. Cairns, 2♂, 2♀ (SAM); ♂, ♀, H. Carter (ANIC); ♂, 3♀, GB, (ANIC); 3♂, ♀ (MV). Cairns district, J. A. Anderson, 5♂, 5♀ (QM). 17.05S, 145.46E, Meringa, 7♂, 6♀ (SAM, MV). 17.06S, 145.47E, Gordonvale: 5.x.1986, on shrubs, J. Rheinheimer, 1♂, 1♀

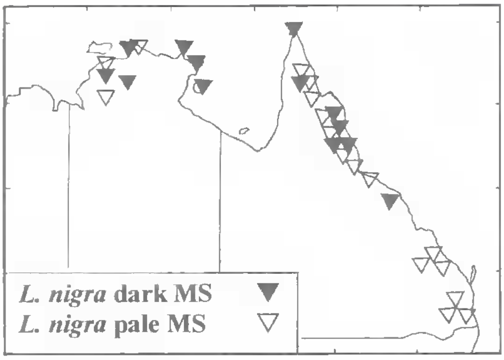

FIG. 25. Records for *Luciola nigra* in northern Australia, showing distribution of mesoscutellum colour.

(ANIC); E. Allen, 1935, 3♂, 2♀ (QM); x.1917, E. Jarvis, ex scrub, 2♂; Gordonvale, Maitland Road, ix.1988, K. Chandler, 6♂, 5♀, on *Acacia* sp. and understory. 17.07S, 145.41E, Little Mulgrave R., HH, 2♀ (AM). 17.07S, 145.47E, Mulgrave R., 4mi. W Gordonvale, 31.xii.1966, DKM, 1♂, 1♀. 17.34S, 145.55E, Coorumba, R. Mulder, 26.iii.1977, 1♀; 15-28.v.1983, 3♂, 6♀.

DIAGNOSIS. One of only two Australian *Pteroptyx*, distinguished from *P. cribellata* by the dimensions of the deflexed elytral apex (Fig. 20J).

DESCRIPTION. Males are redescribed; females are newly described.

Male. 6-8.5mm long. pronotum, MN orange, MS and elytra usually very dark brown, MS sometimes brownish orange; head, antennae and maxillary palpi dark brown, labrum brownish, labial palpi yellow; ventral surface of prothorax yellow, of meso and metathorax brown; legs 1, 2 with yellow coxae and trochanters, remainder dark brown; legs 3 dark brown except for yellow trochanters; basal abdominal sternites dark brown, posterior margin of sternite 5 narrowly pale, and white light organs in sternites 6, 7; all tergites dark brown; dorsally reflexed margins of sternite 6 brown, of sternite 7 white sometimes with small brown patches in anterior fourth.

Pronotum 1.0-1.1mm long, 1.2-1.3mm wide; midanterior margin projecting moderately beyond acute anterolateral angles; lateral margins subparallel, narrowly explanate margins not wider in posterior half; punctures broad shallow, contiguous.

Elytral deflexed apex with sides A and B much longer than side C (Fig. 20J); apex obliquely truncate if viewed from above.

Head deeply depressed between eyes; GHW 1.2-1.5mm; SIW 0.2-0.4mm; ASD > ASW; frons-vertex junction not defined; eye excavation not developed.

Elytral epipleuron continuous to elytral apex; sutural ridge evanescent before apex.

Light organs occupying sternites 6, 7 entirely except for a narrow posterior margin of 7; sternite 7 with dimple, otherwise as described for *P. cribellata* (Fig. 20J). Tergite 8 (Fig. 20L,N) with flanges and lateral ridges similar to *P. cribellata*; aedeagal structure similar to *P. cribellata*.

Female. 6-8mm long. Coloured as for male except MS pale orange or dark brown, light organ restricted to sternite 6 and sternites 7, 8 dark brown. Median posterior margin of abdominal sternite 8 broadly and deeply indented.

REMARKS. Certain Gordonvale specimens (in ANIC) were observed synchronously flashing on and beneath a species of *Acacia* (K. Chandler obs.). 'Flashes were observed at 6-8 second intervals, always with a progressive discharge from one extremity of the bush (usually the top first) over approximately 1 second for the discharge to move around the tree'.

Pyrophanes Olivier

Pyrophanes Olivier, 1885: 368; in Baer, 1886: 132; 1902: 72; 1907: 56; 1911b: 102. McDermott, 1964: 46; 1966: 116. Ballantyne, 1968: 106, 107; 1987b: 173-176. Calder 1998: 180.

TYPE SPECIES. *Pyrophanes similis* Olivier, designated by McDermott, 1966: 116.

DESCRIPTION. MALE. This redescription is based on a generic review of *Pyrophanes* in Ballantyne (1992) and includes morphological characters of non-Australian species.

Dorsal surfaces punctate and clothed in short fine hairs.

Pronotum. W/L 1.7; midanterior margin rounded, usually projecting beyond rounded slightly obtuse anterolateral corners; lateral margins converging anteriorly and posteriorly, or subparallel; lateral margins narrowly explanate, not more widely so in posterior half; posterolateral corners not produced much beyond posterior margin; most of disc smoothly convex, depressed mainly in lateral areas.

Elytra. Punctation not similar to that of pronotum; apices not deflexed; elytra sub-parallel-sided when closed; interstitial lines feebly developed; epipleuron and sutural ridge not extending to elytral apex; elytral apex rounded, not ridged.

Head. Moderately exposed when withdrawn; moderately excavated between eyes; posterolateral eye excavation not developed; GHW about 3 times SIW; labrum transverse; antennal sockets not contiguous, ASD < ASW; frons-vertex junction not defined; eyes widely separated ventrally. Mouthparts well developed; apical segment of labial palpi fusiform, much smaller than apical segment of maxillary palpi. Antennae length subequal to twice GHW or slightly less; 11 segmented; segments simple; scape large, often clavate (Fig. 26I); FS1 subequal in length to pedicel; apex of FS 1 and certain other FS may be produced laterally; all FS except FS1 at least twice as long as wide; apical FS never shortened and club-like, nor produced laterally or flattened.

Legs. MFC present (Fig. 26H); femora 1 and 2 often stout and tibiae 1 and 2 may be curved; femora 3 often enlarged and swollen, and tibiae 3 curved and expanded at their apices (Fig. 26H).

Abdomen. Posterior margin of basal abdominal sternites not recurved. Light organs usually occupying sternite 6 entirely except sometimes for a narrow posterior margin; bipartite (Fig. 26A) in sternite 7, reaching sides but not posterior margin. Sternite 7 MPP short, broad, wider than long and emarginate apically, not upturned or engulfed by the apex of tergite 8; PLP short, narrow and apically rounded; posterior margin between PLP and MPP with a pair of elongate, slender, medially turned lobes bearing hairs on their anterior face only, and paired pointed projections between the lobes and the MPP; a median longitudinal trough is often present between light organ halves; sternite 7 lacks a dimple or median carina and is not swollen or arched in its posterior half; posterior margin densely clothed in fine hairs (not depicted in Fig. 26A). Tergite 8 symmetrical, not shortened, and projecting considerably beyond the MPP; median posterior margin not narrowed or downturned and engulfing the apex of sternite 7; posterior margin medially emarginate; ventral surface (Fig. 26B-D) with a deep median trough which is separated by ridges and flanges from paired lateral troughs bearing anteriorly short spines (area 'a' Fig. 26C) and posteriorly dense hairs (Fig. 26C); medially turned lobes along posterior margin of sternite 7 are below the spined area in resting position.

Aedeagal Sheath. With paraprocts (Ballantyne 1987a: 150, fig. 14a-d). Aedeagus elongate, slender; lateral lobes about 4/5 as long as median lobe, and fused for 1/2-3/4 of their length (Fig. 26E-G).

FEMALE. Known females are macropterous.

LARVA. Lacking laterally explanate margins in *Pyrophanes similis* (Blair, 1927; Bertrand, 1972, 1973).

REMARKS. Olivier (1885) erected *Pyrophanes* for 3 new species, *beccarii*, *appendiculata* and *similis* characterising the male terminal abdomen with a midposterior point or lobe on the terminal sternite. This area is slightly produced (Fig. 26), and apically emarginate, not pointed or lobed. The aedeagal sheath, lying in the median ventral trough of tergite 8, often projects beyond the posterior margin of sternite 7, and is probably Olivier's 'lobe'. Olivier's (1885) plate V, fig.12, and (1907) plate 3, fig. 10 are inaccurate representations of the terminal sternite (Ballantyne, 1992).

McDermott (1964) briefly redescribed *Pyrophanes*: 'may vary toward *Pteroptyx*'. He was probably describing specimens subsequently described as *Pteroptyx macdermotti* McLean (Ballantyne & McLean, 1970). The terminal abdominal segments in *Pyrophanes* are distinctive. McDermott apparently misinterpreted the median visible structure, as had Olivier, and referred to the 'trilobed structure' of the terminal sternite.

An aquatic larva was attributed to *Pyrophanes similis* (Blair, 1927; Bertrand, 1972, 1973).

Pyrophanes beccarii Olivier
(Fig. 26)

Pyrophanes Beccarii Olivier, 1885: 369; 1902: 72; 1907: 56; 1910: 48; 1913: 417.

Pyrophanes beccarii Olivier. McDermott, 1966: 116. Calder 1998: 180.

Luciola complicata Lea, 1921b: 66. Ballantyne in Calder 1998: 180 (synonymy).

TYPES. Holotype. ♂ *Pyrophanes beccarii:* INDONESIA: Aru Islands (MCG). Holotype ♂ *Luciola complicata*: N Qld: 13.52S, 142.51E, Coen R, Cape York Pen. (SAM).

MATERIAL. 2 holotypes and 26 specimens. N QLD: 12.44S, 143.17E, Iron Ra., Cape York Pen., 11-17 May, 1968, GBM, pr in cop (UQ). 12.44S, 143.15E, Claudie R: 2♂ (SAM); 28.i.1914, 2♂ (id as *L. platygaster* by A. Lea), 1♀ (SAM); xi.1912-ii.1913, J. Kershaw, 8♂, 13♀ (MV).

DIAGNOSIS. The only Australian species of *Pyrophanes*, it is distinguished from *P. appendiculata* by its uniformly dark brown elytra and the presence of a lateral expansion of the apex of FS 1.

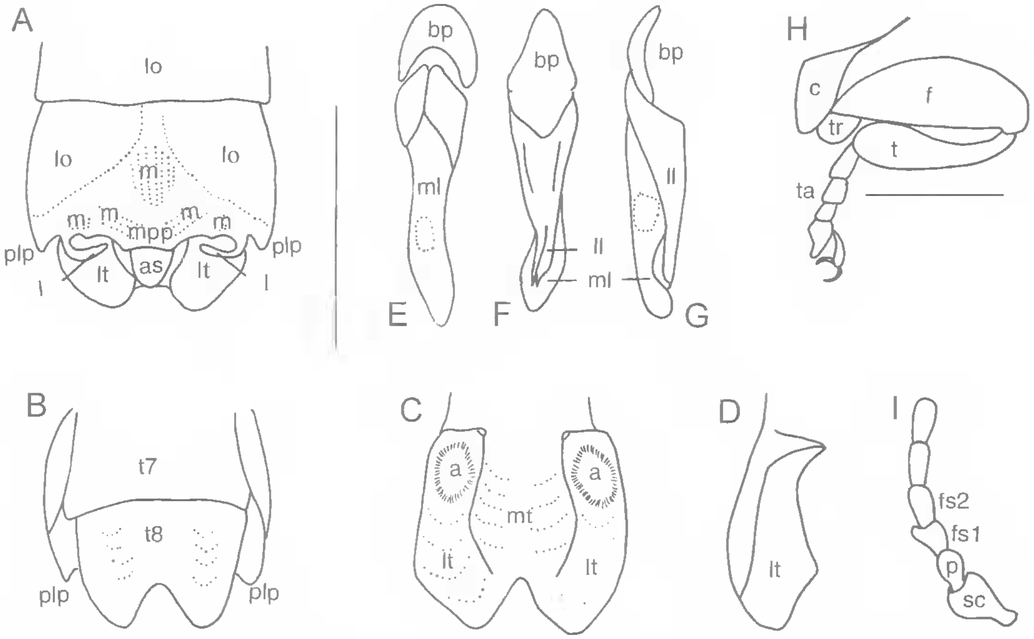

FIG. 26. *Pyrophanes beccarii*, holotype ♂. A,C,D, ventral (A,C) and right lateral (D) aspects of terminal abdominal sternites (A) and tergites (C, D); E-G, aedeagus, ventral, dorsal and left lateral; H, left hind leg, ventral; I, right antenna segments 1-6. Scale lines 1mm; lines shared by: A-G, I. a = area a referred to in text; as = aedeagal sheath; bp = basal piece; c = coxa; f = femur; fs1, 2 = antennal flagellar segments 1, 2; l = lobe of posterior margin of abdominal sternite 7; ll = lateral lobes; lo = light organ; lt = lateral trough of ventral surface of tergite 8; m = muscle; ml = median lobe; mpp = median posterior projection sternite 7; mt = median trough tergite 8; p = pedicel; plp = posterolateral projection sternite 7; sc = scape; t = tibia; ta = tarsus; tr = trochanter; t7, 8 = tergites 7, 8.

DESCRIPTION. *Male*. 6.0-8.0mm long; pronotum, MS and MN pale, semitransparent and yellow; elytra uniformly dark brown in holotype, lateral and sutural margins sometimes finely orange in anterior 1/4 or less; head antennae and palpi brown to black; ventral surface of prothorax yellow, of meso and metathorax brown; legs 1 yellow with brown tibiae and tarsi; coxae, legs 2 and 3 similar, legs 3 sometimes yellow with dark tarsi only; basal abdominal sternites yellow, sternite 5 white or yellow, sternites 6 and 7 white, with light organs confined to sternites 6, 7; posterior margin of sternite 7 golden yellow, ventral surface of tergite 8 yellow; dorsal surfaces of posterolateral projections brown; dorsal abdomen yellow.

Pronotum 1.0-1.2mm long; 1.7mm wide; median anterior margin gently rounded, barely projecting beyond rather acute anterolateral corners; punctures small, shallow, separated by at least the width of a puncture.

Head moderately depressed between eyes; GHW 1.1mm; SIW 0.3mm; ASD < ASW. Antennae (Fig. 26I) with elongate scape, expanded in apical 2/3; pedicel short; FS 1 about as long as pedicel, and produced laterally at apex; FS 2, 3 subequal and slightly expanded at apex; FS 4-9 narrower than FS 1-3; FS 7-9 subequal in length, slightly shorter than FS 4-6; FS 4-9 subequal in width, 4, 5 slightly wider than 6-9. MFC present (Fig. 26H); no specimen shows equal numbers of teeth on both legs, probably as they have broken off; a maximum of 10 teeth was observed on one leg of one specimen; hind femora swollen and slightly curved, hind tibiae curved and swollen at apex (Fig. 26H).

Light organs occupying sternite 6 entirely and bipartite in sternite 7 (Fig. 26A); median ventral face of sternite 7 with median trough and muscle attachments clearly visible through semi-transparent cuticle; ventral surface of tergite 8 (Fig. 26C,D) with area 'A' oval, concave, surrounded by short fine hairs and densely covered with very short semitransparent spines; area 'A' occurs immediately above the medially turned lobes of sternite 7; area 'B' densely clothed with short fine hairs. Aedeagus asymmetrical, with short lateral lobes (Fig. 26E-G).

Female. 5.5-7.0mm long; coloured as for male except venter of body yellow - light brown, white light organ in sternite 6 only and sternites 7, 8 yellow; antennae with FS 1 short, slightly longer than pedicel and not produced laterally; posterior margin of penultimate abdominal sternite broadly excavated; median posterior margin of sternite 9 not excavated.

DISTRIBUTION. In Australia this species occurs only in the central part of Cape York Pen. (Fig. 27).

REMARKS. The function of the developments along the posterior margin of sternite 7 is not known, but certain pinned specimens have this margin, excluding the PLP, inclined vertically such that if the specimen is viewed from beneath the posterior margin of this sternite appears to be entire; in this situation the incurving lobes are adjacent to the spined area of the lateral troughs.

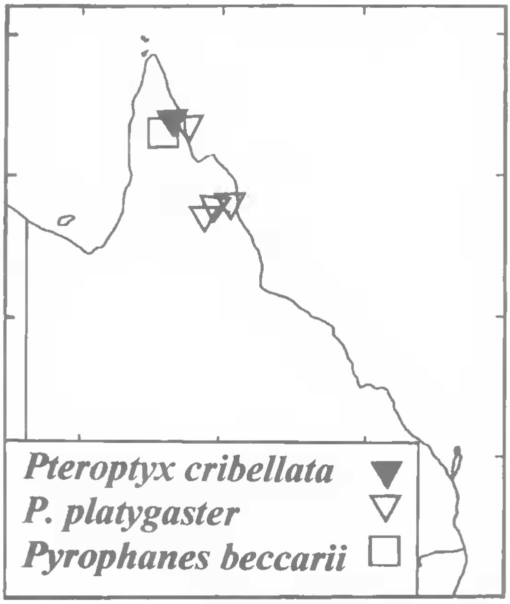

FIG. 27. Records of *Pteroptyx* and *Pyrophanes* in far north Queensland.

SPECIES INCERTAE

Luciola (Luciola) incerta (Boisduval)

Lampyris incerta Boisduval, 1835: 124. Calder, 1998: 180.
Colophotia incerta Dejean, 1837: 104 (catalogue name only).
Luciola incerta (Boisduval). Olivier, 1902: 80.
Luciola (Luciola) incerta (Boisduval). McDermott, 1966: 106.

TYPE. New Holland, not found at MNHP by LB in November 1993.

REMARKS. The described dorsal colour approaches that of *L. dejeani* and *L. costata.* The ventral colouration approaches *dejeani.*

Lampyris serraticornis Boisduval

Lampyris serraticornis Boisduval, 1835: 124; McDermott, 1966: 123. Calder, 1998: 180.

TYPE. New Holland location unknown, not found at MNHP by LB in November 1993.

REMARKS. The described dorsal colour approaches that of *L. dejeani* and *L. costata.*

CLADISTIC ANALYSIS

MISSING DATA. Many authors have discussed computer interpretation of missing data in phylogenetic analyses in the last 10 years. The ready availability of computers to handle such information has led to the widespread use of '?' for not only missing data, but also inapplicable and polymorphisms. Few systematists still use '?' coding for polymorphisms as computer programs are now available that allow polymorphic scoring for taxa. Phylogenetic analyses of data matrices containing large numbers of missing data have been reported in recent times because of the inclusion of: fossils (Gauthier et al., 1988; Messenger & McGuire, 1998; Skevington & Yeates, 2000; Wilkinson, 1995) for which molecular, developmental and many morphological characters cannot be scored; behavioural knowledge (Carpenter, 1987); and molecular data (Chavarria & Carpenter, 1994). One gender of several taxa may be unknown (e.g. Yeates & Lambkin, 1998) and cannot be included in morphological data matrices. This data disjunction (Nixon & Carpenter, 1996), which occurs when there is missing data for characters in the terminal taxa being compared, creates considerable problems in phylogenetic analyses by increasing the number of solutions and reducing the data decisiveness (Goloboff, 1991) of the resulting most parsimonious trees (Nixon & Carpenter, 1996).

Cladistic programs assign states to taxa missing data, based on the most parsimonious distribution of known characters (Novacek, 1992). However large numbers of missing values concentrated in terminal taxa may result in terminal taxa being placed in radically different positions on most parsimonious trees, or trees unstable to the addition of new data (Nixon & Carpenter, 1996), with the resultant strict consensus tree totally unresolved (Carpenter, 1987). Large numbers of missing entries in certain taxa may force taxa into 'branch swapping eddies' that generate huge numbers of most parsimonious trees and decrease resolution of the cladogram (Novacek, 1992). Initial cladistic analyses for 43 species of the Luciolinae exceeded the phylogenetic program limit for the number of most parsimonious trees that could be saved. This problem is due to the large proportion of missing larval and female data in the matrix. Larval features alone (8 characters) are missing for 19 taxa, and female and larval features (up to 16 characters) are missing for a further ten taxa. The removal of nine taxa, for which both the larvae and females are unknown, significantly decreased the numbers of most parsimonious trees.

The removal of taxa with considerable amounts of missing data is contraindicated because poorly represented taxa may still include novel combinations of characters that are important for correctly reconstructing the phylogeny, and contain information on the structure of the tree that cannot be retrieved from the rest of the data matrix (Novacek, 1992). Relationships among terminal taxa are not only affected by the amount of missing data, but also by the relative distribution of that data (Wilkinson, 1995, 1997). Wilkinson (1995) considered the situations where taxa with large numbers of missing values could be safely removed from the analysis, without affecting inferred relationships, tree lengths, or consistency indices. Safe taxonomic reduction involves the removal of taxonomic equivalents (Wilkinson,1995), taxa with missing characters that do not differ with respect to phylogenetically informative characters. No taxonomic equivalents were found in the data matrix, but two taxa missing all female and larval features, differed in only a single homoplasious character from other taxa. Removal of only these two near taxonomic equivalent taxa decreased the number of most parsimonious trees and allowed relationships to be inferred from 41 taxa in four genera of the Luciolinae.

TERMINAL TAXA. There has been no previous attempt to analyse Luciolinae phylogeny using the methods of cladistics. We attempted this analysis as a precursor to further taxonomic work on this fauna, as any analysis on the Australian fauna alone, given that none of the genera is endemic, would yield little information about relationships. The Luciolinae genera and subgenera are presented here largely in the form devised by McDermott (1966).

Specimens of 43 taxa of the Luciolinae were coded for morphological features which clearly distinguished species, groups of species, or genera (Table 1). This analysis included all the Australian species plus a wider taxon sampling of the Luciolinae based where possible on the type species of each genus and subgenus. Alternatively genera were scored from a representative species for which specimens were accessible and/or published information exists. LB scored all but *Photuroluciola* Pic, which was not reliably identifiable in collections. Australian species are indicated by * in Table 1 and Figs 30 and 33. Subgenera are enclosed in parentheses.

A representative collection of New Guinean species considered by Ballantyne (1992) to be closely related to the Australian fauna was included, and two distinctive but as yet unnamed groups from New Guinea code named 'Sisiak' (= '*Luciola* species 12' in Ballantyne, 1987b: 185, fig. 1c-f) and 'MtMissim'. A single female of the latter was described by Ballantyne (1968: 122, figs 130-132, 134) as possibly belonging to *Luciola* (*Pygoluciola*); the species is now known from a single male (Ballantyne, 1992). Also included were certain non-Australian *Pteroptyx* as a basis for comparison with the Australian and New Guinean bent-winged fireflies (Ballantyne & McLean, 1970; Ballantyne 1987a, 1992). Information on non-Australian species presented here is supported by published work (Ballantyne, 1968, 1987a,b; Ballantyne & McLean, 1970; Ballantyne & Buck, 1979) as well as recent examinations. With two exceptions LB examined and dissected reliably identified museum specimens of every non-Australian species recorded specifically for this purpose (specimens are housed in BMNH and ANIC). *Luciola (Pygoluciola) stylifer* and *Pteroptyx macdermotti* are represented by a very few specimens and were scored from published or thesis descriptions only (Ballantyne, 1968, 1987a, 1992). We have included some non-Australian species of *Atyphella*, a genus that extends to New Guinea and neighbouring islands but whose range is not yet defined. McDermott (1964, 1966) did not recognise the genus and in 1966 transferred all these species to *Luciola* subgenus *Luciola*. Ballantyne in Calder (1998) reassigned *Atyphella* to generic level based on seven Australian species including *majuscula* Lea which was transferred from *Luciola*. Nine species currently contained in *Atyphella* are included in our phylogenetic analysis of the Luciolinae.

As all other subfamilies have seven visible abdominal segments in the male, any genus outside the Luciolinae could have served as an outgroup. An undescribed species of a South American *Photuris* was chosen as it has been the subject of recent investigation (Ballantyne, 1992; Lloyd & Ballantyne, in prep.).

We excluded nine species, *Atyphella brevis*, *A. ellioti* sp. nov., *A. flammulans* sp. nov., *A. immaculata* sp. nov., *A. monteithi* sp. nov., *Luciola (Luciola) carolinae*, *L. cowleyi*, *L. dejeani* and *L. (Pygoluciola) stylifer* from two analyses because all female and larval characters are unknown for these taxa.

Atyphella brevis and *A. flammulans* sp. nov. were removed from one analysis because, while missing all female and larval characters, they differ from other taxa by only a single homoplasious, but informative, character.

DATA ANALYSIS. Phylogenetic analyses presented here use the method of cladistics (Hennig, 1966; Farris, 1983). We do not prejudge the relative informativeness of characters nor exclude characters because of their perceived level of homoplasy (Larson & Dimmick, 1993).

Cladistic analyses were performed with polymorphic characters interpreted as 'partial uncertainty'. PAUP chooses a state from the set of available states that allows minimisation of the tree length (Swofford, 1993).

We performed parsimony-based phylogenetic analyses with heuristic searches of the data using 10 random step-wise addition sequences, tree-bisection-reconnection (TBR) branch swapping, MULPARS and branches having maximum length zero collapsed to yield polytomies in effect, using PAUP version 3.1.1 and PAUP* versions 4.0b1a (68K no FPU) and 4.0b2 (Swofford, 1998). These versions of PAUP have a tree-save limitation of 32,676 most parsimonious trees. When this limitation was reached the analysis was repeated using the 'nchuck' command in PAUP to save only 30,000 trees less than, or equal to, a specified length before moving to the next random addition sequence. Strict and semistrict consensus (Bremer, 1990) of the most parsimonious trees were computed using PAUP. Where specified, analyses were repeated using Hennig86 ver. 1.5 (Farris, 1988). The command mh* was used to find initial trees. The trees retained were then passed to the extended branch swapper, bb*. Figures 30-34 were prepared using PAUP, and Fig. 35, showing characters and character states upon a most parsimonious tree, was prepared with CLADOS version 1.2 (Nixon, 1992) with DELTRAN optimisation.

Successive approximations character weighting (successive weighting) was used as a guide to choose between most parsimonious trees (Farris, 1969; Carpenter, 1988). This is an iterative character weighting procedure in which weights are assigned based on their observed level of homoplasy. Initial weights are derived from the most parsimonious trees under equal weighting, and subsequent heuristic searches completed based on the rescaled consistency index (Farris, 1989). The procedure is repeated until the weights (and trees) remain stable over iterations. Successive weighting of the most parsimonious trees was computed using PAUP with a base weight of 1000.

Bremer support (Kallersjö et al., 1992) to indicate character support for nodes on the cladogram was calculated using the computer program TreeRot (Sorenson, 1996). As tree-save limitations were likely to affect calculation of Bremer support, support values were conducted on the data matrix for 42 taxa with polymorphisms removed. Figure 34A indicates support values calculated on the first saved most parsimonious tree. Figure 34B indicates successively weighted support values (Bremer,1994) calculated on the first saved, successively weighted tree.

CHARACTER ANALYSIS. Characters are numbered according to sequence in the data matrix and designated states are numbered to the right. The matrix of taxa and assigned character states is given in Table 1.

ADULT MALE MORPHOLOGY (CHARACTERS 1-88)

Pronotum (1-9)

1. Hypomera. *0.* open. *1.* closed in front.

2. Lateral pronotal margins. *0.* diverging along anterior half or more with some convergence in posterior area (Fig. 1A-D,F,G,I-L). *1.* Subparallel or wider across middle with slight convergence anteriorly and posteriorly. *2.* diverging along their length (Ballantyne & McLean, 1970 fig. 4c). *3.* converging posteriorly along their length (Fig. 19A). In states 0 and 2 the pronotum is wider across the base than across the middle; in state 1 it is wider across the middle than across the base.

3. Anterolateral corners of pronotum. *0.* obliterated (McDermott & Buck 1959, fig. 38). *1.* rounded obtuse (Fig. 1, 19A-E). *2.* pointed (Ballantyne, 1968 fig. 130). *3.* acutely rounded (Ballantyne 1968, fig. 120).

4. Degree of head exposure in front of pronotum. *0.* greatly exposed. *1.* scarce to moderately exposed. *2.* concealed.
The head is either greatly exposed in front of the pronotum (when the head cannot be retracted beneath the pronotum), slightly exposed (when at least some of the posterior section of the head is retracted beneath the pronotum at rest) or concealed (not visible from above).

5. Posterolateral corners of pronotum. *0.* rounded obtuse (Fig. 1A-C,D,F-G,I,J-L). *1.* right angled or angulate obtuse. (Fig. 19C-E; Ballantyne & McLean 1970, fig. 4H). *2.* rounded acute. *3.* broadly pointed (Ballantyne, 1968 fig. 120). *4.* narrowly pointed (Ballantyne, 1968 fig. 130).

6. Posterolateral corners of pronotum. *0.* scarcely projecting beyond posterior margin nor delimited by a deep emargination of the posterior margin. *1.* projecting considerably beyond posterior margin and often delimited by an emargination of the posterior margin (Ballantyne, 1968 figs 20, 33, 38, 51, 62, 70).

7. Lateral margin of pronotum near posterolateral corner. *0.* not indented. *1.* slightly indented.

8. Lateral margin of pronotum. *0.* not flattened. *1.* flattened only in posterior half. *2.* all of lateral margin narrowly flattened but not more so in posterior half. *3.* all of lateral margin narrowly to widely flattened but more so in posterior half of pronotum. *4.* lateral margin widely flattened along its length and anterior area as wide as or wider than posterior area.

9. Anterior margin of pronotum. *0.* not explanate. *1.* narrowly explanate.

Elytron (10-17)

10. Punctation. *0.* not conspicuously larger than pronotal punctation. *1.* conspicuously larger than pronotal punctation.

11. Apex. *0.* not deflexed. *1.* deflexed with apex rounded (Fig. 20J,K).

12. Apex. *0.* not deflexed. *1.* deflexed with sides A, B, C equal (Fig. 20K). *2.* deflexed with sides A, B longer than C (Fig. 20J).

13. Development of epipleuron and sutural apex in apical half of elytron. *0.* no thicker than rest. *1.* considerably thicker than anterior portions.

14. Interstitial lines. *0.* 2-4 well defined lines. *1.* one only defined line (line 3). *2.* no lines well defined.

15. Epipleuron. *0.* extending to apex of elytron. *1.* extending past mid point of elytron but not to apex 1. *2.* extending no further than mid point of elytron.

16. Sutural ridge. *0.* extending to apex of elytron. *1.* evanescent before elytral apex.

17. Margins. *0.* parallel sided. *1.* convex sided.

Head (18-39)

18. Depression of vertex. *0.* minimal. *1.* moderate-deep.

19. Approximation of eyes on ventral surface of head (measured as eye separation taken just behind mouthparts/GHW measured ventrally). *0.* wide separation (0.5 or greater). *1.* close to moderate separation (0.4 or less). *2.* contiguous or almost so.

20. Posterolateral eye excavation (Ballantyne, 1968 figs 144, 147-150). *0.* absent; if slightly developed not visible when head is retracted. *1.* well developed and usually visible even when head is evenly retracted.
A well developed posterolateral eye excavation is at least as wide as long when viewed from the side.

21. Antenna length. *0.* much longer than twice GHW. *1.* > GHW - 2 × GHW. *2.* subequal to GHW.

22. Proximity of antennal sockets. *0.* contiguous. *1.* separated by < 2 × ASW but not contiguous. *2.* separated by at least 3 × ASW.

23. Frons-vertex junction. *0.* not acute (Fig 2A,D,H). *1.* acute (Fig. 2C,F,G,I).

24. Median area of frons vertex junction. *0.* not elevated or indented. *1.* elevated and/or indented (Fig 2F, G).

25. Anterior margin of head. *0.* not prolonged. *1.* prolonged in front of eye for about its width (Ballantyne, 1968 figs 132, 134).

26. Labrum. *0.* approximately twice as wide as long. *1.* about as long as wide.

27. Clypeolabral suture. *0.* flexible. *1.* inflexible, visible. *2.* inflexible and invisible (Ballantyne, 1968 figs 132, 134).
John Lawrence (ANIC Canberra) interpreted the nature of the labrum and clypeus on specimens of *Photuris* and "Mt Missim'.

28. Mouthparts. *0.* functional. *1.* non functional.
Non functional mouthparts have very small apical segments of labial and maxillary palpi, mandibles often do not cross in the median line and the antennal sockets are contiguous.

29. Proximity of eyes above labrum (SIW/GHW). *0.* close (1/6-1/15). *1.* moderately separated > 1/6. *2.* widely separated 1/3 - 1/2.

30. Antennal flagellar segment 1. *0.* as long as or longer than pedicel. *1.* shorter than pedicel.

31. Apex of antennal flagellar segment 1. *0.* not expanded at its outer apex. *1.* expanded at its outer apex.

32. Median area of antennal flagellar segment 1. *0.* not produced. *1.* produced (Ballantyne & McLean, 1970 fig. 18b).

33. Flagellar segments 7-9. *0.* not conspicuously shorter than rest of FS. *1.* conspicuously shorter than rest of FS.

34. Number of segments. *0.* 11. *1.* < 11

35. Flagellar segment 9. *0.* apically rounded. *1.* apically pointed.

36. Flagellar segments 2-8. *0.* not expanded. *1.* expanded at anterior apical angle.

37. Antennal segments. *0.* not flattened. *1.* flattened.

38. Pedicel. *0.* not produced at outer apex. *1.* produced at outer apex.

39. Shape of labial palpi. *0.* fusiform or about as wide as long with inner margin entire. *1.* dentate, laterally flattened. *2.* lunate, inner margins entire.

Legs (40-45)

40. Inner tarsal claw of each leg. *0.* not split. *1.* split.

41. Metafemoral comb (Ballantyne, 1987a fig. 1j). *0.* absent. *1.* present.

42. Femora 3 (Ballantyne & McLean, 1970 fig. 4P). *0.* not swollen. *1.* swollen.

43. Curvature of femora 3. *0.* not curved. *1.* curved along their length (Fig. 26H).

44. Swelling of tibiae 3. *0.* not swollen. *1.* swollen at least at their apices (Fig. 26H).

45. Curvature of tibiae 3. *0.* not curved. *1.* curved (Fig. 26H).

Abdominal Sternites (46-62)

46. Sternite 8. *0.* present. *1.* absent.

47. Light organ in sternite 7. *0.* entire (e.g. Fig. 4A). *1.* posterior medial division short - long. (Ballantyne, 1968 fig. 42, 91). *3.* bipartite (Fig. 26A).

48. Light organ in sternite 7. *0.* reaching sides and posterior margin of sternite 7. *1.* reaching sides but not posterior margin. *2.* not reaching sides or posterior margin.

49. Size of light organs. *0.* occupying at least half of the area of sternite 7 or more. *1.* restricted to very small paired anterolateral plaques that occupy less than 10% of the area of sternite 7. (Ballantyne & McLean, 1970 fig. 18C).

50. Apex of MPP of sternite 7. *0.* MPP not developed. *1.* apex truncate. *2.* apex rounded. *3.* apex gently emarginate (e.g. Fig. 20D,F,J,K,I). *4.* apex deeply emarginate (Fig. 3D,E,G,J; Ballantyne, 1968 fig. 13).

51. Length/width of MPP of sternite 7. *0.* not produced. *1.* about as long as broad or shorter; narrower than half the width of sternite 7. *2.* about as long as broad; at least half as wide as sternite 7. *3.* at least twice as long as wide.

52. MPP of sternite 7. *0.* not engulfed (e.g. Fig. 4A). *1.* partially engulfed and surrounded laterally by the slightly downturned apex of tergite 8. (Ballantyne, 1968 figs 5, 9, 26, 91). *2.* engulfed by the down turned apex of tergite 8 completely (Ballantyne, 1968 figs 18, 107-109, 111, 113).

53. Median longitudinal carina in sternite 7. *0.* absent. *1.* present (Ballantyne & McLean, 1970 fig. 3D,F).

54. Median longitudinal trough in sternite 7. *0.* absent. *1.* present.

55. Median longitudinal trough on ventral surface of MPP. *0.* absent. *1.* present (Ballantyne & McLean, 1970 fig. 3D, F).

56. All of sternite 7, especially in posterior half. *0.* flat, not arched or swollen (e.g. Fig. 4A). *1.* arched and often swollen (Ballantyne, 1968 figs 56, 89).

57. Length of PLP of sternite 7. *0.* not developed. *1.* slightly produced (Fig. 26A). *2.* moderately produced, may extend beyond the tip of the MPP. *3.* considerably produced (Ballantyne 1987b, fig. 2A, B).

58. Width of PLP of sternite 7. *0.* not developed. *1.* narrower than MPP (Fig. 26A). *2.* as wide as MPP (Ballantyne & McLean, 1970 fig. 9A,B). *3.* broader than MPP (Ballantyne, 1987b fig. 2A,B).

59. Inclination of PLP of sternite 7. *0.* not developed. *1.* horizontal. *2.* oblique - vertical (Ballantyne & McLean, 1970 fig. 3D, F; Ballantyne, 1968 figs 11, 13).

60. Incurving hairy lobes along posterior margin of sternite 7 (Fig. 26A). *0.* absent. *1.* present.

61. Pointed projection of sternite 7 posterior margin (Fig. 26A). *0.* absent. *1.* present.

62. Dimple on sternite 7 (Fig. 20K). *0.* absent. *1.* present.

Abdominal Tergites (63-69)

63. Ventral face of tergite 8. *0.* lacking flanges. *1.* with symmetrical flanges (Fig. 20I). *2.* with asymmetrical flanges.(Ballantyne, 1987a fig. 13R).

64. Ventral face of tergite 8 with depressed lateral troughs (Fig. 26C,D). *0.* absent. *1.* present.

65. Ventral face of tergite 8 with elongate longitudinal symmetrical developments margining a median longitudinal trough. *0.* absent. *1.* fine transparent barely elevated ridges margining a median longtitudinal trough. *2.* slightly thickened barely elevated ridges margining a median longtitudinal trough. *3.* low barely elevated ridges present in posterior half of ventral surface only. *4.* longtitudinal raised well developed ridges delimiting a median longitudinal trough.

66. Ventral face of tergite 8 with asymmetrical projections (other than flanges), and/or transverse ridges and/or hooks. *0.* absent. *1.* present (Ballantyne, 1987b fig. 2F). Ballantyne 1987b termed all the narrowed ventral projections of tergite 8 'flanges'. Flanges are here interpreted as the narrowed anterior projections often of lateral longitudinal ridges on the ventral surface of tergite 8.

67. Bifurcate anterior margin of tergite 8. *0.* about as long as or no longer than entire posterior (visible) part of tergite. *1.* at least 3 times as long as entire posterior visible part of tergite.

68. Width of tergite 8. *0.* about as wide as long. *1.* very short. *2.* much longer than wide and projecting considerably beyond MPP.

69. Width of posterior half of tergite 8. *0.* not narrowed, or lateral margins converging but not abruptly. *1.* abruptly narrowed (Ballantyne, 1968 figs 17, 110, 112, 114).

Aedeagal Sheath (70-73)

70. Symmetry of aedeagal sheath sternite. *0.* symmetrical in posterior half (Fig. 21B,D,E). *1.* asymmetrical in posterior half (Fig 21I).

71. Length/width of aedeagal sheath. *0.* never more than about 4 times as long as wide. *1.* very long and narrow (about 7 times as long as wide).

72. Lateral margins of aedeagal sheath. *0.* lacking paraprocts (Fig. 21C,D). *1.* with paraprocts (Fig. 21A,B).

73. Length/width of tergite 9 of aedeagal sheath. *0.* about as long as wide. *1.* much wider than long.

Aedeagus (74-84)

74. Maximum width across lateral lobes/ maximum width of median lobe. *0.* wide (4 – 6/1) (Ballantyne 1968, fig. 171). *1.* moderate (2/1) (Fig. 5). *2.* narrow (less than 2/1) (Fig. 21O,R,U; 26E).

75. Inclination of apex of median lobe. *0.* not curving ventrally. *1.* curving ventrally (Ballantyne, 1968 figs 164, 168).

76. Extent of preapical ventral area of median lobe. *0.* not produced. *1.* produced and rounded. *2.* produced and pointed (Ballantyne, 1968 figs 162, 164, 168).

77. Length of median lobe of aedeagus relative to lateral lobes. ***0***. much shorter than LL. ***1***. subequal in length to lateral lobes or slightly longer. ***2***. longer than LL but less than twice their length. ***3***. much longer than LL i.e. more than twice their (separated) length.

78. Separation of lateral lobes of aedeagus. ***0***. separated for > half their length. ***1***. separated for less than half their length (Fig. 26E-G).

79. Width of lateral lobes of aedeagus. ***0***. wider and flatter at apices than widest point of ML (Fig. 21L, M). ***1***. about as wide at apices as widest point of ML (Fig. 5). ***2***. narrower at apices than ML widest point (Figs 21P, S,U,V; 26E-G).

80. Separation of lateral lobes into broad basal section and narrowed widely separated apical section. ***0***. no such separation. ***1***. present (Fig. 21K).

81. Aedeagal symmetry. ***0***. symmetrical. ***1***. asymmetrical (Fig. 26E, F).

82. Fleshy lobes on lateral lobes. ***0***. absent. ***1***. present as short rounded projections (Fig. 21K). ***2***. present as elongate leaf like lobes (Fig. 21L,N).

83. Extent of ventral face of apices of lateral lobes. ***0***. beyond sides of ML, visible from beneath (Figs 5, 21K-M). ***1***. not beyond ML sides, invisible from beneath (Figs 21O, P,R,S,U,V; 26E-G).

84. Lateral appendages of lateral lobes. ***0***. absent. ***1***. present (McDermott & Buck 1959, fig. 62A-C; McDermott, 1962 fig. 1A-C).

Male Colour Patterns (85-88)

85. Colour of pronotum. ***0***. pronotum concolourous. ***1***. pronotum with dark markings.

86. Colour of elytral margins compared to rest of elytra. ***0***. elytra concolourous (dark – light brown). ***1***. if elytron dark then only lateral margin pale. ***2***. lateral and sutural margins pale at least in basal half. ***3***. lateral and sutural margins pale with base of elytron dark. ***4***. lateral sutural and apical margins pale, base of elytron pale. ***5***. if elytron pale then darker markings scattered at base and apex. ***6***. if elytron pale then dark markings at apex only. ***7***. elytra concolourous (pale).

87. Colour of interstitial lines 1, 2 as distinct from basal elytron colour or colour of its margins. ***0***. no paler than dark area between lines 1 and 2. ***1***. about as pale or slightly paler. ***2***. distinctly paler than this area so l lines appear as stripes.

88. Colour of terminal abdominal tergum. ***0***. as dark as or darker than preceding terga. ***1***. pale (as pale as preceding terga or paler).

Adult Female Morphology (89-96)

89. Development of fore wings of female. ***0***. fully developed (or covering all but two abdominal segments). ***1***. elytra longer than pronotum but shortened such that they cover approximately 1/2-2/3 of the abdomen. ***2***. elytra shorter than pronotum (more than half as long as pronotum) and contiguous in the median line. ***3***. elytra shorter than half pronotal length and often contiguous or closely approaching in the median line. ***4***. elytra shorter than half pronotal length and widely separated in the median line. Macropterous gravid females may have one to two abdominal segments protruding beyond the elytral apices.

90. Development of hind wings of female. ***0***. fully developed. ***1***. hind wings about 2/3 as long as macropterous state. ***2***. hind wings vestigial or absent.

91. Extent of female light organ. ***0***. occupying sternites 6 and 7. ***1***. restricted to sternite 6.

92. Colour of pronotum. ***0***. pronotum concolourous. ***1***. pronotum with coloured markings.

93. Colour of elytra. ***0***. elytra concolourous. ***1***. elytra not.

94. Number of elytral interstitial lines. ***0***. four. ***1***. less than 4.

95. Nature of pronotal punctures. ***0***. contiguous in at least lateral areas. ***1***. not contiguous in any area.

96. Head form. ***0***. of winged female form (Fig. 6B). ***1***. of wingless female form (Fig. 6D, E).

Larval Morphology (97-104)

97. Production of lateral margins of terga. ***0***. lateral margins not explanate (Fig. 22). ***1***. lateral margins narrowly explanate especially at posterolateral corners (Ballantyne, 1968 figs 158-160). ***2***. lateral margins widely explanate (Figs 12, 15).

98. Length/width of pronotum. ***0***. longer than wide. ***1***. about as long as wide.

99. Nature of tergal margins. ***0***. not ridged. ***1***. ridged.

100. Paired dorsal and ventral tubercles on protergum. ***0***. absent. ***1***. present (Fig. 15A,C).

101. Shape of posterolateral corners of protergum. ***0***. rounded (Fig. 15A-C). ***1***. acute (Fig. 12C). ***2***. narrowly produced.

102. Margins of median line on terga 1-10. ***0***. not ridged. ***1***. ridged.

103. Size of punctures in anterior half of terga 2-10. ***0***. no larger than rest. ***1***. larger than rest.

104. Extent of posterolateral corners of tergum 11. ***0***. not produced (Fig. 7A, 15B). ***1***. produced (Fig. 12A-C, 15A,C).

CHARACTER DESCRIPTIONS. The data matrix (Table 1) describes 104 characters for 44 taxa. Many taxa were coded missing, '?', because females and/or larvae are unknown for many species. Larval characters alone (8 characters) are missing for 19 taxa, all female and larval characters (total of 16 characters) are missing for a further 9 taxa, and 14 female and larval characters are missing for one further taxon. Thirty-four characters are multistate; 23 have three states, 6 four states, 5 five states, and one character has eight states. Multistate characters 4, 14-15, 19, 21-22, 27, 29, 48, 52, 57-58, and 89-90 were treated as additive as they include states describing linear variation of size or development. The data matrix includes polymorphic coding (characters with more than one state observed in specimens of a taxa) for 14 taxa and seven characters. The minority state is indicated

TABLE 1. Data matrix describing 104 characters for 44 taxa including polymorphic coding. The minority state is indicated by placement in a separate row beneath the majority state for that particular character and taxon. * = Australian species.

	10	20	30	40	50	60	70	80	90	100	
Photuris sp.	0001000410	0000211000	0100001011	0000000021	0000000000	0000000000	0000000000	0000001010	0001112000	0111100100	0000
Atyphella aphrogeneia	1011000300	0010000110	1100010000	0000000000	0000017?02	1000000000	0000000001	0001001010	0000100100	1100000100	0001
Atyphella atra *	1011000300	0000000110	2010040100	0100000000	0000010100	1000000000	0000000001	0001001010	0000100102	1111012100	0000
										00	
Atyphella brevis *	1011000100	5000001110	2010010?00	0000000000	0000010102	1000000000	0000000001	0001001010	00001321??	??????????	????
Atyphella carolinae	1011000300	0000000120	?100010?00	0000000010	0000001?02	1000000000	0000000001	0001001010	000010????	??????????	????
Atyphella conspicua *	1011000300	0000000110	2111010000	0000000000	0000010102	1000000000	0000000001	0001001010	0000100132	111111????	????
			1								
Atyphella costata	1111000300	0000000110	3100010010	0000000010	0000020102	1000000000	0000000001	0001001010	0000061100	101000????	????
	0										
Atyphella ellioti *	1011000300	0000000110	2100010?00	0001000000	0000010102	1000000000	0000000001	0001001010	0000111???	??????????	????
Atyphella flammans *	1011000300	0000001110	2000010?00	0000000010	0000010102	1000000000	0000000001	0001001010	0000132101	1110012100	0001
Atyphella flammulans *	1011000300	0000001110	2010010?00	0000000010	0000010102	1000000000	0000000001	0001001010	0000132???	??????????	????
Atyphella immaculata *	1011000300	0000000110	2100020000	0000000000	0000010102	1000000000	0000000001	0001001010	00000001??	??????????	????
Atyphella inconspicua *	1111000300	0000000110	2110010000	0000000000	0000010102	1000000000	0000000001	0001001010	0000100132	111101????	????
	0								1		
Atyphella leucura	1011000300	5000000110	1100010000	0000000010	0000010102	1000000000	0000000001	0001001010	0000151???	???????1??	????
Atyphella lewisi *	1011000300	0000001110	2000010100	0000000000	0000010?2?	1000000000	0000000001	0001001010	0000132141	1001??????	????
Atyphella lychnus *	1012000300	0000000110	2100010100	0000200000	0000010102	1000000000	0000000001	0001001010	0000111102	1100012110	0101
									2		
Atyphella marginipennis	1011000300	0000000110	1100010010	0000000010	0000010102	1000000000	0000000001	0001001010	0000101100	1011002100	0011
Atyphella majuscula *	1011000300	0000001110	1100010000	0000000010	0000010102	1000000000	0000200001	0001001010	0000000100	1000002110	1011
Atyphella monteithi *	1012000300	0000001110	2100010000	0000000000	0000010001	1000000000	0000000001	0001001010	00001001??	??????????	????
Atyphella olivieri *	1011000300	0000001110	1000010?00	0000000010	0000010002	1000000000	0000000001	0001001010	0000130101	1110002111	0101
Atyphella scintillans *	1011000300	0000000110	2100010000	0001000000	0000010002	1000000000	0000000001	0001001010	0000100122	1100012111	0111
Atyphella similis *	1011000300	0000000110	2110010000	0000000000	0000010102	1000000000	0000000001	0001001010	0000100132	1101012100	0011
									1		
Atyphella wolfi	1011000300	0000001110	2100010000	0000000010	0000010102	1000000000	0000000001	0001001010	0000030100	1010102???	????
Atyphella tuomensis	1012011300	0000000110	2000010000	0000000010	0000011103	3100010000	0000300001	0001001010	0000151100	1111005???	????
Atyphella obsoleta	1012011300	0000000110	3100010000	0000000010	0000010102	3100010000	0000300001	0001001010	0000151100	1111007???	????
Bourgeoisia hypocrita	1111000300	0000111121	2000010000	0000000010	000001???0	0000000000	0000000000	0000121000	0200000112	1001001010	1010
			1								
Colophotia praeusta	1011100200	0002100110	1100000020	0010100000	0000012204	301010?320	0010401000	1102001120	0010061100	101100????	????
Curtos costipennis	1011000201	0001000110	1100000010	0000000010	0000010202	0000000000	000000010?	0011001010	0000061100	101100????	????
Lampyroides syriaca	1311100200	0002100111	2100010010	0000001000	0000010?02	2000000000	0000000000	0000121010	0?00170112	1101111???	????
Luciola (Luciola) australis *	1111100200	0002110110	1100000010	0000000000	0000010103	1000000000	0000400000	0002001020	0010000100	1001000000	0001
	2										
Luciola (Luciola) cowleyi *	1119100300	0000100121	2000010000	0000000000	0000010200	0000000000	0000000000	0000000021	0100110???	??????????	????
	5										
Luciola (Luciola) dejeani *	1111000200	0002100110	1100000010	0000000010	0000010000	0000000000	0000000000	0000131000	020006110?	??????????	????
Luciola (Luciola) flavicollis *	1111100200	0002100110	1100000010	0000000000	0000010203	1000000000	0000400000	0002001020	0010020000	1011000000	0001
	1					3			41		
Luciola (Luciola) italica	1011000200	0002110110	1100010010	0000000010	0000010000	0000000000	0000000000	0000131000	0200000100	100100????	????
Luciola (Luciola) nigra *	1111100200	0002100110	1100000010	0000000000	0000010201	1000000000	0000400000	0002001020	0010000000	1001000000	0001
	3				1 2						
Luciola (Luciola) orapallida *	1111100200	0002100110	1100000010	0000000000	0000010201	1000000000	0000400000	0002002020	0010025100	1011000000	0001
	3										
Luciola (Hotaria) parvula	1011000200	0002100110	1100010?10	0000000010	0000010100	0000000000	0000000000	0000121000	0200100112	110101????	????
Luciola (Pygoluciola) stylifer	1?11300200	000??90130	0120000037	0000000010	0000110201	3200000000	00?0???01?	00?1000010	0000161???	??????????	????
Pyrophanes beccarii *	1111100200	0002110100	1100000010	1000000000	1111112103	1001001112	1001400000	0102002120	1010000100	100110????	????
										1	
Pteroptyx cribellata *	1111100200	1102010110	1100000010	0000000000	0000010103	1000001?10	0110400000	0002001020	0010000700	100100????	????
Pteroptyx macdermotti	1111100200	1102010010	1100000020	1000000100	1000012214	1000001111	1001000700	0102002120	0010061100	1011??????	????
Pteroptyx malaccae	1111100200	1102010100	1100000010	1000000000	1001010102	100000?240	0000400000	0102002120	0010061100	100100????	????
						[illegible]					
Pteroptyx platygaster *	1111100200	1202010110	1100000010	0000000000	0000010103	1000001210	0110400000	0002001020	0010000000	1001002???	????
Sisiak	1211210300	0000000110	1000010000	0000000010	0000012102	3001000000	0000010001	0000002020	1010172100	1100007???	????
Mcmissia	1211400100	0000000100	0200123020	0000010010	0000010202	3100001110	0000100000	0001111010	1200071100	1001007???	????

by placement in a separate row in Table 1, beneath the majority state for that particular character and taxon. PAUP (Swofford 1993), unlike Hennig86 (Farris 1988), can accept this polymorphic character scoring.

Character distributions are discussed in terms of the cladogram from the cladistic analysis (Fig. 35). Clades referred to are species-groups identified in the cladistic analysis and defined in Fig. 30.

RESULTS. Cladistic analyses of the entire data matrix of 44 taxa and 104 characters of equal weight, with *Photuris* sp. designated as the outgroup, could not be completed because of the tree-save limitation in PAUP. Several random-addition heuristic searches would finish but the tree-save limitation would be reached before all 10 searches completed. Repeated attempts to analyse the data matrix showed that trees of length 336 were present. Use of the nchuck command (Swofford 1993) to save only 30,000 trees of length less than, or equal to, 336 before moving to the next replicate retrieved 10,866 most parsimonious trees of tree length 336, consistency index (Kluge & Farris 1969) 0.53, consistency index excluding uninformative characters 0.48, retention index (Farris 1989) 0.70, and rescaled consistency index 0.40. We were not confident that all most parsimonious trees of length 336 had been found, nor that these were the most parsimonious trees. Strict and semistrict consensus of the trees of length 336 were identical and well resolved, and indicated the presence of three clades within the Luciolinae (Fig. 30).

The large number of most parsimonious trees is generated because of missing data (see introduction above). The data matrix assembled for this study included a considerable amount of missing data for certain taxa. We excluded nine species from further analyses, because both female and larvae are unknown. Analysis of the 104 characters for the 35 taxa, with 100 random

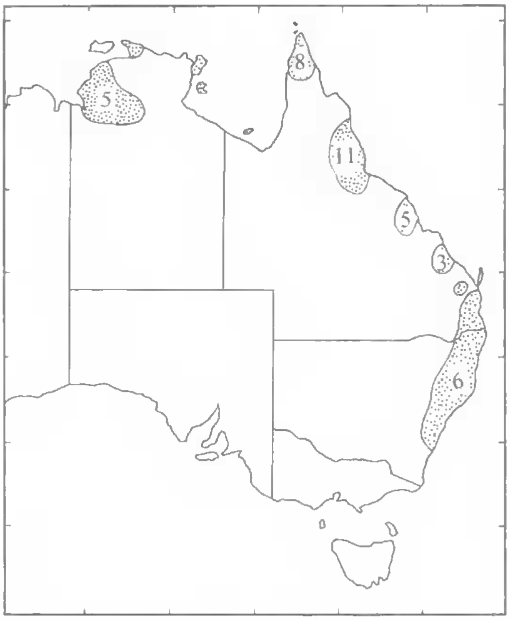

FIG. 28. Distribution of fireflies in Australia (figures show number of species in each zone).

additions, generated 138 most parsimonious trees of tree length 301, consistency index 0.56, consistency index excluding uninformative characters 0.51, retention index 0.71, and rescaled consistency index 0.40. The semistrict consensus (Fig. 31A) shows the same three clades as found in the analysis of all 44 taxa. Successive weighting recovered 15 trees, however the strict (Fig. 31B) and semistrict consensus of these 15 successively weighted trees show a quite different arrangement of the ingroup, with the small medial *Curtos* clade, of Mt Missim and *Curtos costipennis*, dividing and moving basally.

Removal of taxa with considerable amounts of missing data is not advisable because information supporting relationships may be removed (Novacek, 1992) and instead safe taxonomic reduction (Wilkinson, 1995, 1997) was considered. However no taxonomic equivalents could be identified. *Atyphella brevis* and *A. lewisi*, and *A. flammulans* sp. nov. and *A. flammans* differ by a single homoplasious, but informative character, 23. *Atyphella brevis* and *A. flammulans* sp. nov. only, were excluded from the next analysis, as this should have less effect on inferred relationships than the removal of nine taxa. Analysis of the 104 characters for the 42 taxa, with 10 random additions, generated 5,586 most parsimonious trees of tree length 334, consistency index 0.54, consistency index excluding uninformative characters 0.48, retention index 0.70 and rescaled consistency index 0.38. The identical strict and semistrict consensus (Fig. 32A) show the same three clades found in the analysis of all 44 taxa, but with slightly different arrangements in the *Atyphella* clade. Successive weighting recovered 294 trees. The identical strict (Fig. 32B) and semistrict consensus of these 294 successively weighted trees also shows the same three clades.

We were concerned that the presence of polymorphisms may have contributed to the large number of most parsimonious trees generated. An analysis was made of the entire 44 taxa with polymorphisms removed. The majority state was maintained in taxa that had been coded as polymorphic, and the minority state (shown in the rows below the majority state in Table 1) removed. This analysis generated 20,411 most parsimonious trees of tree length 317, consistency index 0.50, consistency index excluding uninformative characters 0.44, retention index 0.70 and rescaled consistency index 0.35. The strict and semistrict consensus (Fig. 33A) show the same three clades as found in the analysis of all 44 taxa with polymorphisms included. Successive weighting of the most parsimonious trees recovered the 78 trees, and the strict and semistrict consensus (Fig. 33B), of these 78 successively weighted trees shows the same three clades as in the unweighted analysis.

As near taxonomic equivalents, *Atyphella brevis* and *A. flammulans* sp. nov. were excluded from an analysis of the data matrix without polymorphisms. Analysis of the 104 characters, with polymorphisms removed, for the 42 taxa, with 10 random additions, generated 1,029 most parsimonious trees of tree length 315, consistency index 0.50, consistency index excluding uninformative characters 0.44, retention index 0.70 and rescaled consistency index 0.35. The identical strict (Fig. 34A) and semistrict consensus show the same three clades as found in the analysis of all 44 taxa without polymorphisms. Successive weighting recovered 78 trees. The strict and semistrict consensus (Fig. 34B) of these 78 successively weighted trees also show the same three clades.

As Hennig86 is unable to process polymorphic scorings, the most parsimonious tree to show characters and character states was selected from the analysis of the entire data matrix without

	NEW GUINEA	TORRES STRAIT 1	NORTHERN PENINSULA 2	MID PENINSULA 3	COOKTOWN - MOSSMAN 4	CAIRNS - ATHERTON 5	KIRRAMA - CARDWELL 6	PALUMA RANGE 7	TOWNSVILLE MT ELLIOT 8	PROSERPINE - EUNGELLA 9	BYFIELD - ROCKHAMPTON 10	BULBURIN - MARYBOROUGH 11	GYMPIE - BRISBANE 12	BORDER RANGES 13	NEW ENGLAND - DORRIGO 14	CARRAI - BARRINGTON 15	SYDNEY - ILLAWARRA 16	NSW SOUTH COAST 17	EAST GIPPSLAND 18	DANDENONG - OTWAYS 19	TASMANIA 20	NORTHWEST AUSTRALIA	NORTHERN TERRITORY
Atyphella atra													—	—									
Atyphella brevis					—	—																	
Atyphella conspicua					—	—																	
Atyphella costata		—		—																			—
Atyphella ellioti									—	—													
Atyphella flammans					—	—	—			—													
Atyphella flammulans						—																	
Atyphella immaculata					—	—																	
Atyphella inconspicua					—	—																	
Atyphella lewisi					—																		
Atyphella lychnus													—		—	—	—						
Atyphella majuscula	—			—																			
Atyphella monteithi						—																	
Atyphella olivieri					—	—	—	—															
Atyphella scintillans												—	—	—	—	—							
Atyphella similis														—	—								
Luciola australis									—	—	—												
Luciola cowleyi																							—
Luciola dejeani																							—
Luciola flavicollis	—		—	—	—	—	—		—	—	—	—	—										—
Luciola nigra	—	—	—	—	—	—	—	—		—		—	—	—								—	—
Luciola orapallida				—																			
Pteroptyx cribellata	—		—	—																			
Pteroptyx platygaster				—	—	—																	
Pyrophanes beccarii	—			—																			
TOTAL	5 [2]	2	3	8	10	11	4	2	3	5	2	3	5	4	3	2	1					1	5 [1]

FIG. 29. Table summarising distribution of the Australian Lampyridae in alphabetical and taxonomic sequence. Presence of each species in the north-south sequence of geographic zones is indicated by the solid horizontal bar.

polymorphisms and with the two near taxonomic equivalent taxa removed. Strict and semistrict consensus of both weighted and unweighted analyses were used as a guide to choose the preferred most parsimonious tree (Fig. 35).

DISCUSSION

SAFE TAXONOMIC REDUCTION. With taxa containing considerable proportions of missing characters (over 70%), and missing some characters in all 25 taxa, Wilkinson (1997) using parsimony analysis with PAUP version 3.1.1 (Swofford, 1993) generated over 30,000 most parsimonious trees. The removal of three taxonomically equivalent taxa, while still retaining taxa with over 65% missing data generated 456 most parsimonious trees. Wilkinson (1995) considered that taxonomic equivalent taxa could be removed from the analysis without affecting inferred relationships, tree lengths, or consistency indices. However it is obvious that removal of taxonomic equivalents from the matrix may result in changes in tree length and consistency indices if the taxa removed contain autapomorphs.

The removal of the nine taxa that contained the largest proportion of missing data significantly decreased the number of most parsimonious trees generated during analysis. While resolution increased in parts of the *Luciola/Pteroptyx* clade in the consensus tree, resolution was lost in the *Atyphella* clade. Removal of only two near taxonomic equivalents also decreased the number of most parsimonious trees generated, but not as significantly, and resolved some sections of the *Atyphella* clade.

The presence of polymorphic taxa also increased the number of most parsimonious trees. Recoding of these taxa for majority states allowed a slight increase in the resolution of the consensus trees. A slight improvement in resolution was also observed in the consensus trees for the analysis with polymorphisms and two near taxonomic equivalents removed.

Successive weighting, by decreasing the weight of the homoplasious characters, can lead to changes in topology and resolution. The only significant changes to topology that can be attributed to successive weighting occurred after removal of nine taxa from the data matrix. The support for the *Curtos* clade is based on homoplasious characters. Downweighting of those characters, together with the removal of one of the three taxa, removed the support for the grouping and allowed the remaining two taxa to split and move. Increased resolution in the consensus trees was observed in all successively weighted analyses. Except for the analysis with nine taxa removed, the successively weighted continue to show the same three, well resolved, monophyletic clades.

The effect of successive weighting on polymorphic and multistate characters has not been

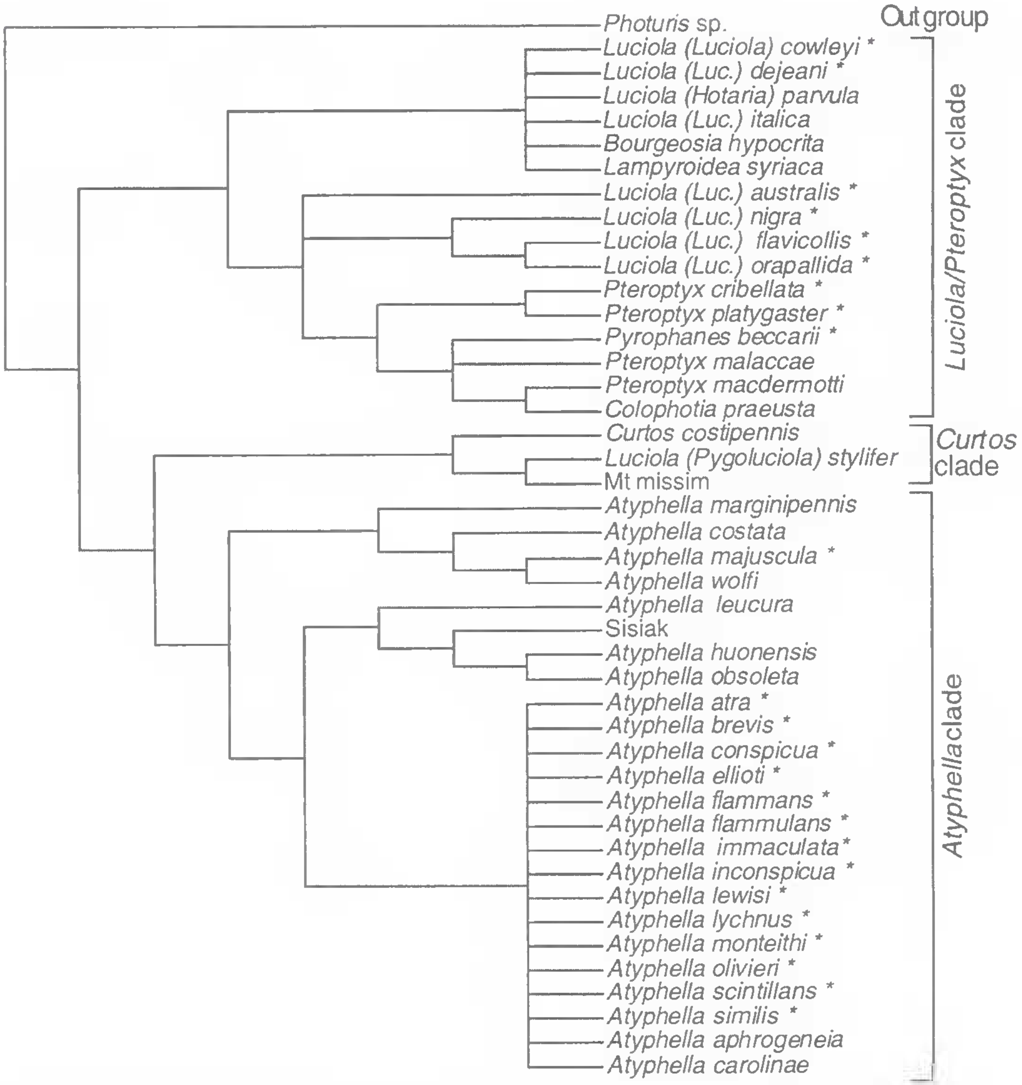

FIG. 30. Strict and semistrict consensus of 10,866 most parsimonious trees for the entire data matrix, including polymorphisms, of 44 taxa.

investigated. Successive weighting downweights the homoplasious characters. If homoplasy is confined to a single state in a multistate character or one of the morphs in a polymorphic character, the rescaled consistency index, upon which the successive weighting is based, falls and the entire character is downweighted. The data matrix for this phylogenetic study of the Luciolinae contains 34 multistate characters, and seven coded as polymorphic across 14 taxa. A direct comparison can be made on the consensus trees for the analyses with two near taxonomic equivalents between the consensus trees for the analysis with polymorphisms (Fig. 32) and the consensus trees for the analysis with polymorphisms removed (Fig. 34). Removal of polymorphisms allowed *B. hypocrita* and *L. cowleyi* to form a clade and the position of *Py. beccarii* to be clarified. Successive weighting without polymorphisms shows greater resolution of the relationships in the *Atyphella* than the successive weighting of the data matrix including

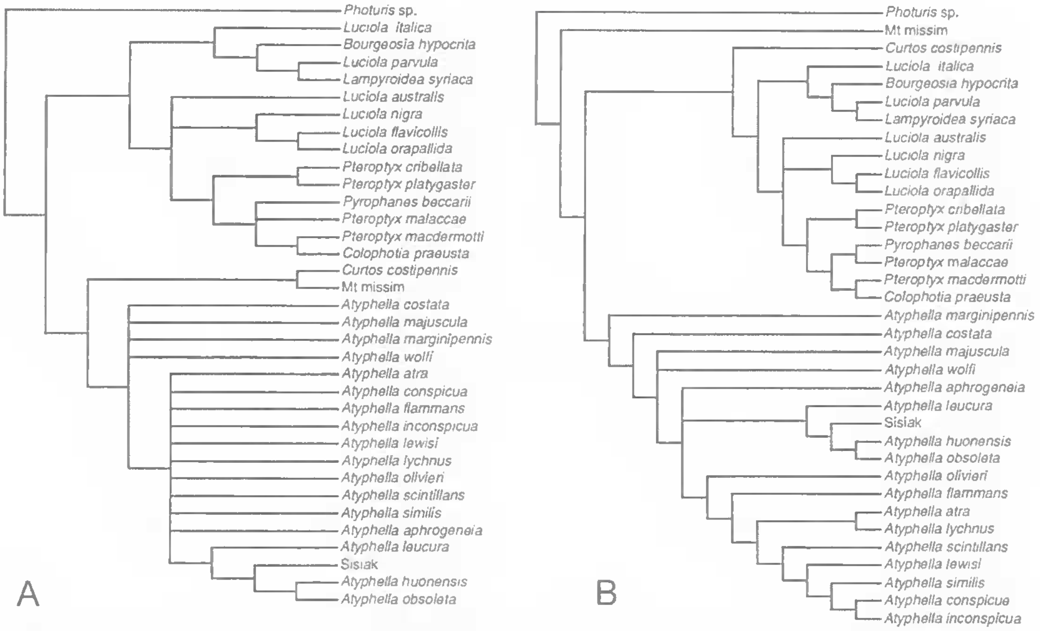

FIG. 31. Effect of removing nine taxa missing all female and larval characters. A, semistrict consensus of 138 most parsimonious trees for the data matrix, including polymorphisms, of 35 taxa. B, strict and semistrict consensus of the 15 successively weighted trees from the 138 most parsimonious trees for the data matrix, including polymorphisms, of 35 taxa.

polymorphisms. The presence of polymorphic taxa does not only significantly increase the number of most parsimonious trees, but also decreases the resolution of consensus trees from both equally weighted and successively weighted analyses.

THE LUCIOLINAE. Three monophyletic clades (Fig. 30) are recognised in the Luciolinae. Basally the *Luciola/Pteroptyx* clade includes *Luciola (Luciola) australis*, *L. (L.) cowleyi*, *L.(L.) dejeani*, *L. (L.) flavicollis*, *L. (L.) italica*, *L. (L.) nigra*, *L. (L.) orapallida*, *Luciola (Hotaria) parvula*, *Pteroptyx cribellata*, *Pter. macdermotti*, *Pter. malaccae*, *Pter. platygaster*, *Bourgeosia hypocrita*, *Lampyroidea syriaca*, *Colophotia praeusta*, and *Pyrophanes beccarii*. Medially the *Curtos* clade is comprised of Mt Missim, *Curtos costipennis* and *L. (Pygoluciola) stylifer*. The terminal *Atyphella* clade includes *Atyphella aphrogeneia*, *A. atra*, *A. brevis*, *A. carolinae*, *A. conspicua*, *A. costata*, *A. ellioti* sp. nov., *A. flammans A. flammulans* sp. nov., *A. inmaculata*, *A. inconspicua*, *A. leucura*, *A. lewisi*, *A. lychnus*, *A. majuscula*, *A. marginipennis*, *A. monteithi*, *A. olivieri*, *A. scintillans*, *A. similis*, *A. wolfi*, *A. huonensis*, *A. obsoleta* and Sisiak.

The same three clades are found in all analyses except the successively weighted analysis with the removal of the nine taxa missing all female and larval characters. In this successively weighted analysis the medial clade changes position and splits, Mt Missim becoming basal to the Luciolinae and *Curtos costipennis* joining the *Luciola/Pteroptyx* clade basally (Fig. 31B). *Luciola (Pygoluciola) stylifer* and Mt Missim form a well supported group in all analyses that include both species. The inclusion of *Curtos costipennis* in the clade is poorly supported, as is the clade itself (Figs 34A, B). As the clade is grouped by three homoplasious characters, of which two involve elytral colour patterns, low Bremer supports result.

The *Luciola/Pteroptyx* clade contains two well-supported clades in all analyses: viz. *Lampyroidea syriaca*, *Bourgeoisea hypocrita*, *Luciola italica*, *L. (L.) dejeani*, *L.(L.) cowleyi*; and *Luciola (Hotaria) parvula*, and *Luciola (Luciola) australis*, *L. (L.) flavicollis*, *L. (L.) nigra*, *L. (L.) orapallida*, *Pteroptyx cribellata*, *Pter. macdermotti*, *Pter. malaccae*, *Pter. platygaster*, *Colophotia praeusta*, and *Pyrophanes beccarii*. These clades present confused subgeneric,

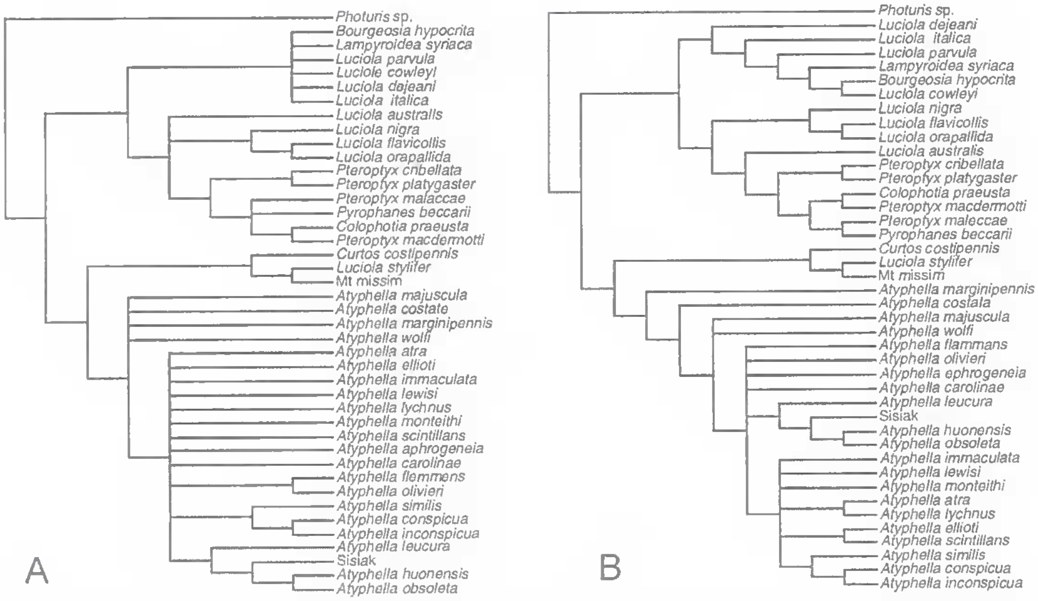

FIG. 32. Effect of removing two taxa, missing many values, that differ from other taxa in one homoplasious character. A, strict and semistrict consensus of 5,586 most parsimonious trees for the data matrix including polymorphisms, of 42 taxa. B, strict and semistrict consensus of the 294 successively weighted trees from 5,586 most parsimonious trees for the data matrix including polymorphisms, of 42 taxa.

generic and family relationships, which may be resolved by the future inclusion of further species in each category.

This analysis supports the generic status of *Atyphella*. McDermott's transfer of *Atyphella* species to *Luciola* subgenus *Luciola* in 1966 is not vindicated. *Atyphella* is now considered to include the following 23 species (six originally described as *Luciola* species): Australian species; *atra* Lea, *brevis* Lea, *conspicua* sp. nov., *costata* (Lea), *ellioti* sp. nov., *flammans* Olliff, *flammulans* sp. nov., *immaculata* sp. nov., *inconspicua* (Lea), *lewisi* sp. nov., *lychnus* Olliff, *majuscula* (Lea), *monteithi* sp. nov., *olivieri* lea, *scintillans* Olliff, *similis* sp. nov.: non-Australian species; *aphrogeneia* (Ballantyne), *carolinae* Olivier, *huonensis* (Ballantyne), *leucura* Olivier, *marginipennis* (Guérin), *obsoleta* Olivier, *wolfi* (Olivier). While the *Atyphella* clade is supported by three homoplasious characters, none involving colour, the posterior asymmetry of the aedeagal sheath sternite is a clear synapomorphy for the group.

Ballantyne (1968) erected *Pygatyphella*, as a subgenus of *Luciola*; distinguished by its distinctive abdominal modifications, but named for its similarities to *Atyphella*. This study shows a close relationship between two species of *Luciola* (*Pygatyphella*) (viz. *obsoleta* Olivier and *huonensis* Ballantyne) and *Atyphella*, and all species of this subgenus should be investigated. However based on these results a well-supported species-group within *Atyphella* contains *obsoleta*, *huonensis*, *leucura* and the undescribed Sisiak.

DISTRIBUTION. Distributional patterns for Australian fireflies are presented as a map of locality records for the whole of Australia (Fig. 28), maps of locality records for individual species in each genus (Figs 8-11, 13-14, 16-18, 23-25, 27) and tabulation of the extent of species through defined regions along the eastern seaboard of Australia (Fig. 29). The rainforests of far north Queensland have been well collected and the data reveal what must be a very fair picture of firefly distribution in those areas. Other areas are less clear.

McDermott & Buck (1959) remarked on the paucity of Australian Lampyridae, contrasting the Jamaican fauna where there are about 50 distinct species. They considered *Luciola* species were probably recent immigrants from New Guinea, and that Australia was isolated since the late Cretaceous probably before the lampyrids

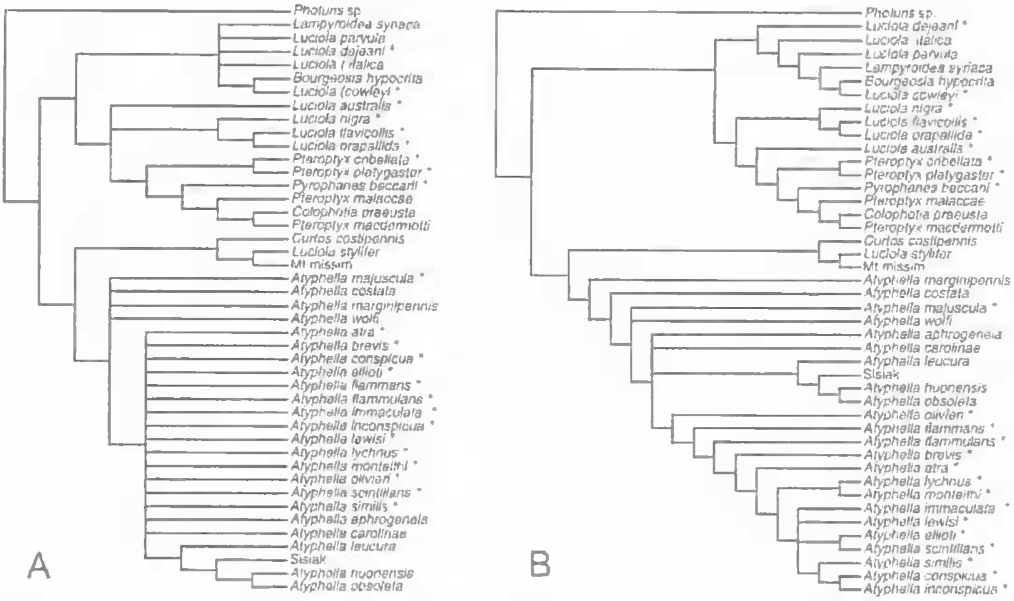

FIG. 33. Effect of polymorphisms. A, strict and semistrict consensus of 20,441 most parsimonious trees for the entire data matrix with polymorphisms removed, of 44 taxa. B, semistrict consensus of the 78 successively weighted trees from the 20,441 most parsimonious trees for the data matrix with polymorphisms removed, of 44 taxa.

had spread sufficiently to be represented in the endemic fauna.

So little is known of much of the *Luciola* of the Oriental Region that a discussion of distribution and possible origins of Australian representatives is inappropriate here. Other groups are better known. While *Atyphella* occurs outside Australia in New Guinea and the western Pacific, almost all of the *Atyphella* treated here are Australian endemic. *Pteroptyx* and *Pyrophanes* occur in New Guinea, Indonesia and Malaysia, and only *Pteroptyx platygaster* is restricted to Australia (Ballantyne & McLean, 1970; Ballantyne, 1968, 1987a, 1992).

This discussion of distribution will concentrate on the eastern coast of Australia where fireflies occur from islands of the Torres Strait south to Kiama in NSW, with their distribution largely paralleling the distribution of rainforest and/or mangroves. Monteith (1997) overviewed the distribution of rainforests and possible natural barriers along the east coast and this treatment owes much to that overview.

Only 2 species are known from mangroves, *Luciola orapallida* in Cape York Pen. and *L. australis*, which occurs from Townsville to Bundaberg. Both have slim bodied active larvae which may be able to move more easily through the mud and slime of this habitat.

The far north tropical area has the most diverse fauna. The narrow coastal strip east of Coen in Cape York Pen. and the Iron Range area support the most species from any part of Australia. This is the rainforest system which Darlington (1961) named the 'mid-Peninsula' region. Monteith (1997) showed it also has the richest local fauna of Aradidae in Australia. Six species, *Pyrophanes beccarii*, *Pteroptyx cribellata*, *Atyphella majuscula*, *Luciola nigra*, *L. flavicollis* and *L. orapallida* occur here. Five also occur outside Australia, and of these, three, viz. *Pyrophanes beccarii*, *Pteroptyx cribellata* and *A. majuscula*, may be recent immigrants from New Guinea, as they are not known farther south. *Luciola orapallida* occurs in mangrove and salt-water couch, where it may replace *L. australis*, which occurs in a similar habitat further south. *Pteroptyx*, which is widely distributed in New Guinea (Ballantyne, 1987a) occurs as far south as Innisfail. Only *L. nigra* and possibly *L. flavicollis* have a much wider distribution along the eastern Australian coast as far south as the southeast corner of Queensland. All of these six 'mid-Peninsula' species have winged females.

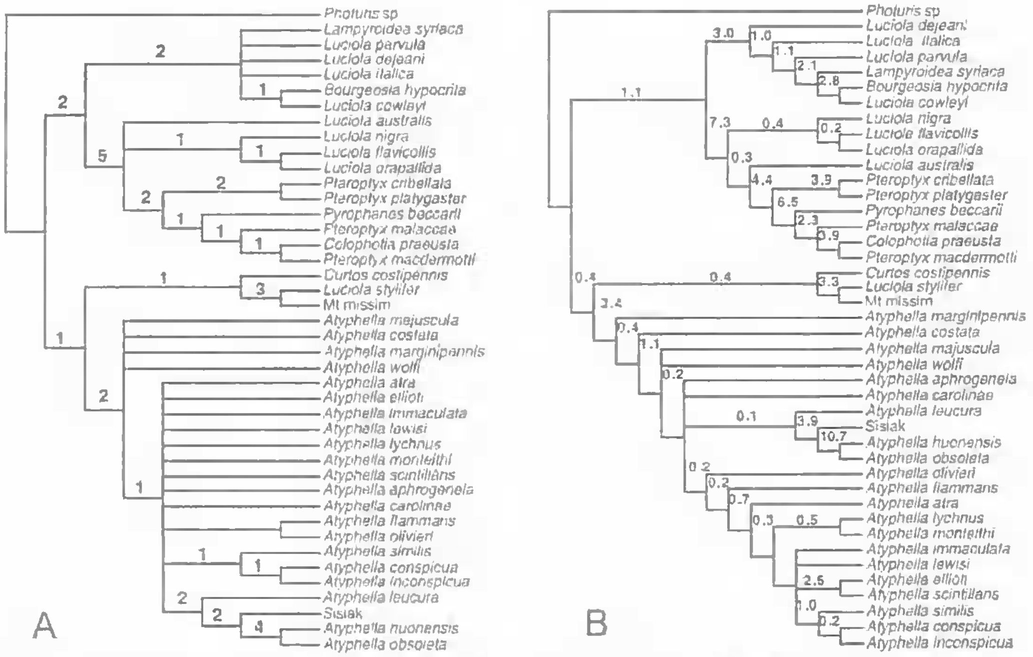

FIG. 34. Effect of polymorphisms and removing only two taxa, missing many values, that only differ from other taxa in one homoplasious character. A, strict and semistrict consensus of 1,029 most parsimonious trees for the data matrix with polymorphisms removed, of 42 taxa. Two species were excluded that only differ from other taxa in one homoplasious character. Bremer support values indicated calculated on the first saved most parsimonious tree. B, strict and semistrict consensus of the 78 successively weighted trees from 1,029 most parsimonious trees for the data matrix including with polymorphisms removed, of 42 taxa. Bremer support values indicated calculated on the first saved successively weighted tree.

South of the central peninsula two different patterns emerge, that of *Atyphella* in association with rainforest tracts, and of certain *Luciola* which appear to be widely distributed in more open forest and not restricted by rainforest tracts.

Atyphella species may have entered Australia several times. A recent influx of *A. majuscula* is restricted to the far north in Cape York Pen. An older element became widely distributed along the east coast before the rainforest corridor became so restricted. In eastern Australia there are now 2 distinct groups of this older element separated by a dry Mackay to Bulburin barrier. The wet tropical group (north of Cooktown to Eungella) has 9 *Atyphella* species, all endemic to this area. They occur mainly in rainforest and five species (all with flightless females with advanced wing loss) are known from above 400 metres (Figs 8-11, 13, 16). Two species are coastal (*flammans* is widespread while *monteithi* is known only from the Cairns area). *flammulans* is known from coastal and higher regions, and *olivieri* has a wide distribution through the wet tropics as far south as Paluma and occurs from sea level to above 1,000 metres. Of these *flammans* and *olivieri* have females in which the hind wings are abbreviated.

In the block south of Rockhampton 4 species occur (Figs 14, 17, 18): they are associated with cooler temperate rainforest of the type which was widespread and shared by other southern continents before the break-up of Gondwanaland. Of these the *A. lychnus* female may have acquired its flightlessness fairly recently and it has a wide and discontinuous distribution in SE Qld and NE and central NSW. However *A. similis* and *A. scintillans*, which have brachelytral females, have a wide distribution. Only *A. atra* is relatively confined.

Species of *Luciola* fall into three distributional groups. Most are not apparently restricted by rainforest boundaries and where known the female is winged and capable of flight.

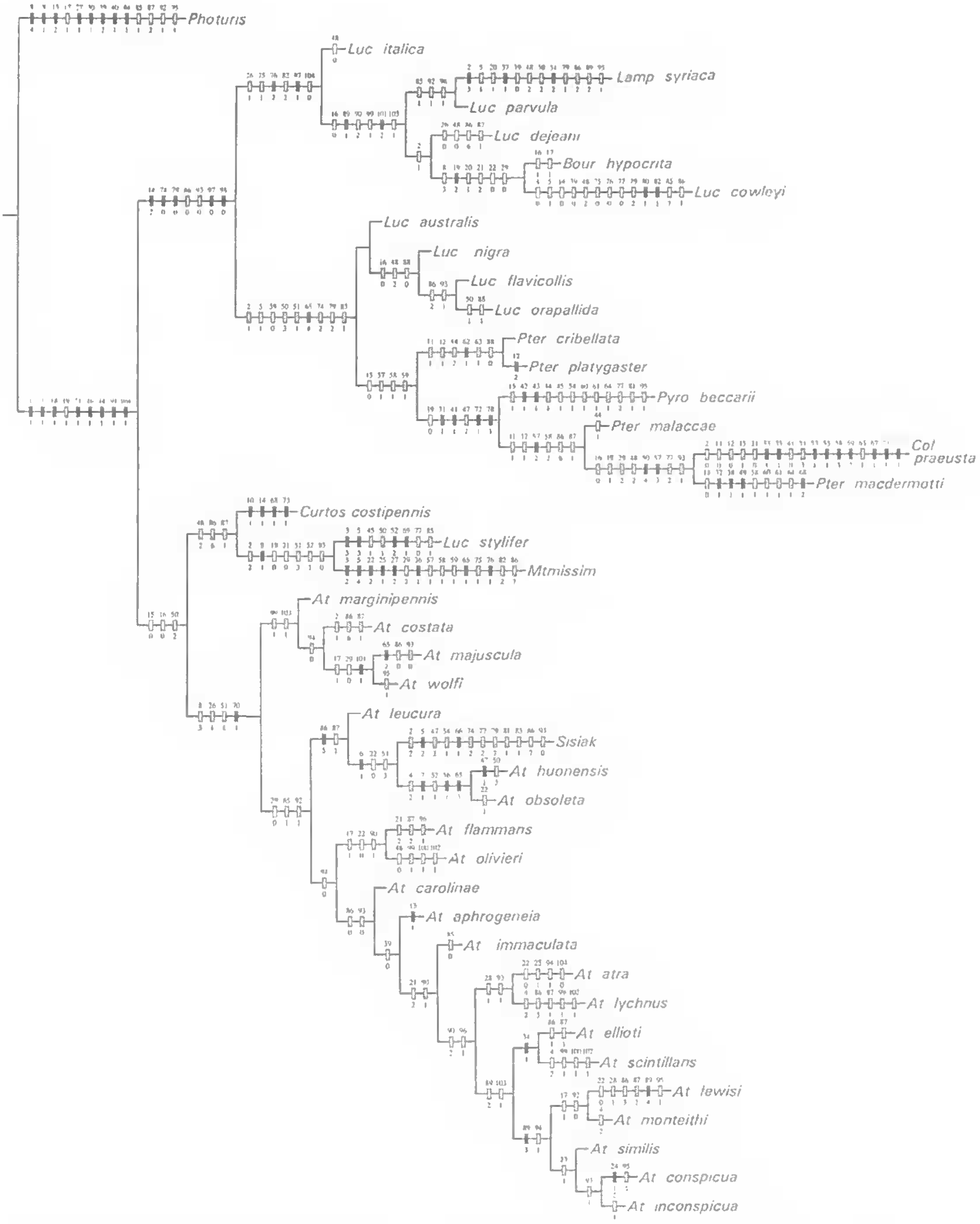

FIG. 35. Preferred most parsimonious tree for the entire data matrix with polymorphisms removed, of 42 taxa, showing characters and character states. White blocks, reversal without homoplasy; black, forward change without homoplasy; stippled, homoplasy.

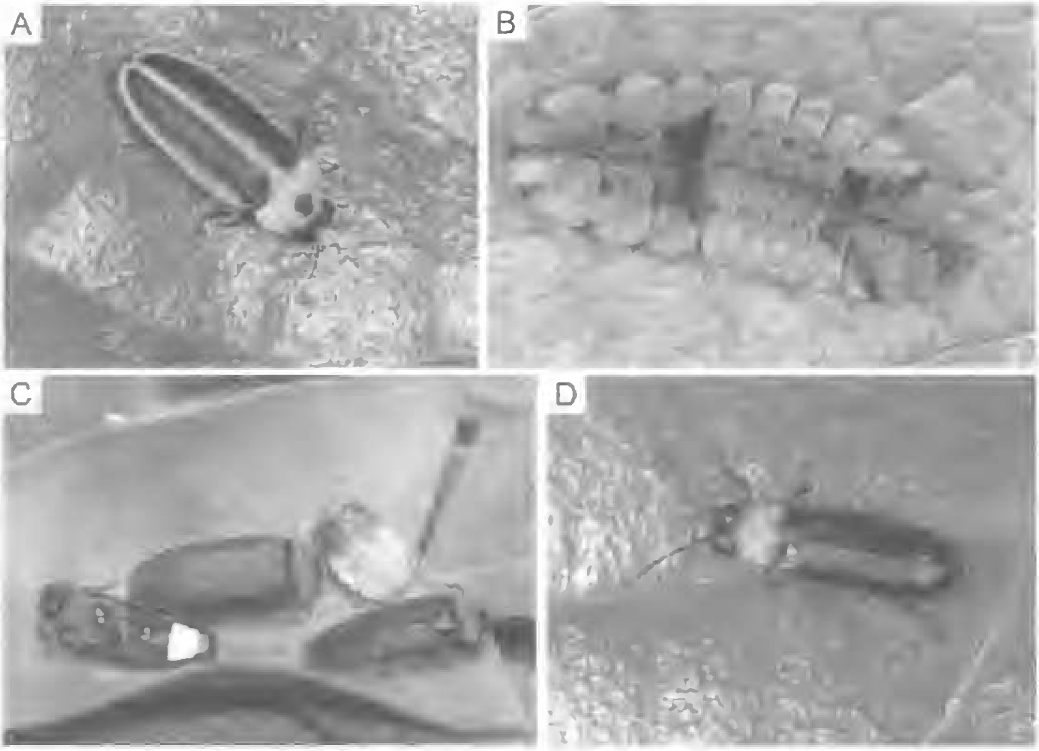

FIG. 36. Living Australian fireflies. A, *Atyphella olivieri*, adult ♂; B, *Atyphella flammans*, larva; C, *Atyphella scintillans*, three macropterous ♂♂ and one brachypterous ♀; D, *Luciola nigra*, adult ♂. (Photos A, B, D, Jeff Wright, QM; C, Bruce Cowell, QM)

L. dejeani may not be Australian. Its distinctive dorsal colouration is shared with *A. costata* and at least 40 other *Luciola* species in Asia and Indomalaysia (McDermott, 1966).

L. cowleyi (Fig. 23) is reliably known only from the Northern Territory where it seems to occur along rivers. The female is unknown.

The third group includes *L. nigra* and *L. flavicollis* (Figs 23-25) which occur across the north of Australia and extend into southeast Qld. They appear to be restricted only by tropical and warm temperate climates and not by rainforest distribution as for *Atyphella*. Both occur in New Guinea (Ballantyne, 1992). Males fly readily, and females can fly. While *L. nigra* has been collected from rainforest and relict rainforest, *flavicollis* is known only from more open sclerophyll forest (LB observations). *L. nigra* flies with *A. scintillans* in the Brisbane area, and at Burleigh Heads NP in an area of rainforest, but it may have flown into the latter area rather than being restricted to it. *L. flavicollis* is very widely distributed across northern Australia, from Cape York to SE Qld and west at least to Carnarvon, and is often attracted to light (LB observations) although LB has never observed it flying in numbers exceeding five.

FEMALE APTERY. McDermott & Buck (1959: 14) considered apterous females likely to develop in high wind areas, wing degeneracy a specific character rather than being common to groups of species, and that the first step is an alate female that seldom flies. Some observations of known behaviour in Australasian fireflies both support and contradict their position.

A. aphrogeneia, the 'surf firefly', has a winged and flighted female living in a precarious position in the surf spray zone (Ballantyne & Buck, 1979; Lloyd, 1973a). Australian observations (Powell, 1964; Ballantyne, 1992) indicate that females rarely fly once a mate has been selected. *Luciola australis* females crawl up low vegetation with head uppermost and may even flex the abdomen so that the light shines upwards. Flashes of females on the ground or low vegetation may be reflected from leaf surfaces or transmitted through the pale abdomen and are easily seen from above. No *Luciola* female from the Australian and Indomalaysian area is flightless. Flightless *Atyphella* females behave similarly (LB's observations on interactions in Lamington and Mt Glorious NP).

In Australia wingless females occur only in *Atyphella*. In the northern tropics where barriers to distribution may be altitude as well as discontinuity of rainforest (Monteith, 1997) those species with the most restricted distribution have brachelytral females (females are not associated for all species however). Species with females where the wing loss is restricted to a shortening of the hind wings (e.g. *olivieri*, *flammans*) have a wider, often somewhat discontinuous distribution which may reflect a more recent loss of flight ability. On the other hand, where the rainforest is not separated by such major barriers in SE Qld and NE NSW, three species of *Atyphella* (all with flightless females) are widely distributed.

COLOUR PATTERNS. Dorsal colour patterns may be a response to external factors. The conspicuous orange pronotum and brown or black elytra common in New Guinea occurs in *Pteroptyx*, *Pyrophanes*, four *Luciola* (two from tropical mangrove areas, two from open forest in tropical and warm temperate areas) and two tropical *Atyphella* and is interpreted as warning colouration (Ballantyne, 1968, 1992). Only two species have a yellow body with dark elytral apices, seen widely in Indomalaysia (McDermott, 1966).

Atyphella spp. from rainforest have colour patterns which will disrupt or confuse their outlines e.g. dark pronotal markings, striped or pale margined elytra. The human eye does not easily detect these insects in the daytime (LB observations).

MORPHOLOGY AND BEHAVIOUR. Ballantyne (1987b) discussed many lucioline morphological modifications and made behavioural inferences. The *Atyphella* male pronotum conceals the head from above and, as eyes occupy much of the ventral head area, vision is directed down in flight. Males actively searching on the ground protrude their heads (Ballantyne, 1992). The more exposed head of *Pteroptyx*, *Pyrophanes* and *Luciola* may allow extra head mobility, and greater visual acuity thus predisposing them to aerial interactions.

Leg modifications occur only in *Pyrophanes* males, which have a metafemoral comb. Lloyd (1979a) surmised its function (in *Pteroptyx*) to kick aside the female elytra before copulation.

Deflexed elytral apices in *Pteroptyx* correlate with abdominal modifications in *P. valida* where the female abdomen is clamped between the elytral apices and the MPP of sternite 7 (the 'copulation clamp' of Lloyd et al. (1989), Wing et al. (1983) and Ballantyne (1987a). The wider occurrence of such behaviour among other species with deflexed elytral apices is not known.

Abdominal modifications may reflect the necessity for muscle attachment related to complex mating protocols involving abdominal flexion (Ballantyne, 1987b, 1992). A bipartite or abbreviated light organ in sternite 8 provides surface area for longitudinal muscle attachment (muscles are visible through the semitransparent cuticle). Such potential flexibility in *Pteroptyx* species is demonstrated by the forward arching of the posterior margin of ventrite 4 (Ballantyne, 1987a: fig. 3a; Ballantyne, 1992) providing a base for muscle attachment. By contrast, Australian *Atyphella* with entire light organs in sternite 7, no forward arching of basal ventrites and no apparent modifications to tergite 8 are assumed to have simpler mating interactions (Ballantyne, 1987b). All *Atyphella* have pale terminal tergite(s) through which the light can be seen clearly. Both species of *Pteroptyx* and two *Luciola* species have very dark terminal tergites so the main light source will only be seen from below unless the abdomen is flexed.

Eberhard (1985) indicated the correlations that exist between genitalic diversity, or lack of it, and sexual characters developed on the terminal abdomen and elsewhere. Many lucioline males belong to his category where secondary body parts (e.g. elytral apices) are used to copulate and morphological variation in these is wide, whereas the primary genitalic structures do not diverge. Similarities between the aedeagal structure of the two Australian species of *Pteroptyx* and certain *Luciola* (*nigra*, *flavicollis*) are offset by species-specific differences in abdominal sternite 7, as well as by the deflexed elytral apex in *Pteroptyx*.

Pyrophanes males exhibit features of the male terminal abdomen and leg modifications, which may be secondary sexual characters (Ballantyne, 1987b). The aedeagus appears to be fairly uniform (Ballantyne, 1992).

The uniform aedeagus structure among most *Atyphella* is not related to secondary sexual characters as the terminal abdomen exhibits uniformity of structure. Few records herein show more than two *Atyphella* species sympatric in time and space.

ASSOCIATION OF FEMALES AND LARVAE. Distribution has been used to associate some larvae and females with males. Most adults are collected while flashing. Unless a flightless female is accidentally taken in leaf litter she will only be collected because her light is seen. She can be associated with males flying at the same time and place (if there is only one species present). No such inference can be made for larvae, which are unpredictable in their light production. In few cases have larvae been reliably associated by rearing.

ACKNOWLEDGEMENTS

Ballantyne thanks the many curators for the loan of specimens, in particular Geoff Monteith at QM who constantly provided new specimens through his own activities in North Queensland, and not unintentionally, inspired the desire to see the completion of this paper. Geoff also provided much helpful advice and criticism on drafts of this paper. Ballantyne is especially indebted to Chris Lambkin who generously donated her time, enthusiasm and expertise in running the cladistic analysis, and is most grateful for this invaluable assistance in helping bridge the cladistic 'generation gap'. John Lawrence interpreted morphological features of several unusual Luciolinae and gave advice about the nature of the labrum in fireflies. Keith Chandler provided behavioural information. This project began as a MSc thesis (by Ballantyne as Powell) at the University of Queensland under the supervision of the late Dr T.E. Woodward, and was revised and extended at the School of Agriculture at Charles Sturt University. Both institutions provided much needed support.

LITERATURE CITED

ARMITAGE, R. W. 1908. Notes on the Queensland Firefly Beetle, *Luciola flavicollis*. The Victorian Naturalist 25(2): 28-30.

BAEHR, M. 1995. Revision of *Philipis* (Coleoptera: Carabidae: Bembidiinae), a genus of arboreal tachyine beetles from the rainforests of eastern Australia; taxonomy, phylogeny and biogeography. Memoirs of the Queensland Museum 38(2): 315-381.

BALLANTYNE, L.A. 1968. Revisional Studies of Australian and Indomalayan Luciolini (Coleoptera, Lampyridae, Luciolinae). University of Queensland Papers, Department of Entomology, University of Queensland Press II no. 6: 103-139.

1987a. Further Revisional Studies on the firefly genus *Pteroptyx* Olivier (Coleoptera: Lampyridae: Luciolinae). Transactions of the American Entomological Society 113: 117-170.

1987b. Lucioline Morphology, Taxonomy and Behaviour: A Reappraisal. (Coleoptera, Lampyridae). Transactions of the American Entomological Society 113: 171-188.

1988. The identities of *Luciola australis* (F.) and *L. guerini* Laporte (Coleoptera: Lampyridae). Journal of the Australian Entomological Society 27: 161-165.

1992. Revisional studies on flashing fireflies (Coleoptera: Lampyridae: Luciolinae: Luciolini). Unpubl. PhD thesis, University of Queensland, St Lucia.

BALLANTYNE, L.A. & BUCK, E. 1979. Taxonomy and behavior of *Luciola (Luciola) aphrogeneia*, a new surf firefly from Papua New Guinea. Transactions of the American Entomological Society 105: 117-137.

BALLANTYNE, L.A. &. McLEAN, M.R. 1970. Revisional studies on the firefly genus *Pteroptyx* Olivier (Coleoptera: Lampyridae: Luciolinae: Luciolini). Transactions of the American Entomological Society 96: 223-305.

BLACKBURN, T. 1897. XXI. Further notes on Australian Coleoptera, with descriptions of new genera and species. Transactions and Proceedings of the Royal Society of South Australia 21: 28-39.

BERTRAND, H.P.I. 1972. Lampyridae. Pp. 598-603. In Larves et Nymphes des Coléoptères Aquatiques du Globe. (Paris).

1973. Part XI. Larvae and Pupae of Water Beetles collected from the Island of Ceylon. (Lampyridae: 100-111). Bulletin of the Fish Research Station, Sri Lanka (Ceylon) 24 (1, 2): 95-112.

BLAIR, K.G. 1927. An aquatic lampyrid larva from S. Celebes. Transactions of the Entomological Society of London Part 1. 75: 43-45.

BOISDUVAL, J.B.A.D. 1835. Voyage de découvertes de l' Astrolabe, exécuté par ordre du Roi, pendant les années 1826-1829, sous le commandement de M. J. Dumont-D'Urville. Faune entomologique de l'océan Pacifique. Deuxième partie. Coléoptères et autres ordres. (J Tastu: Paris).

BREMER, K. 1990. Combinable component consensus. Cladistics 6: 369-372.

1994. Branch support and tree stability. Cladistics 10: 295-304.

BUCK, J., BUCK, E., HANSON, F.E., CASE, J.F, METS, L. & ATTA, G.J. 1981a. Control of flashing in fireflies IV. Free run pacemaking in a synchronic *Pteroptyx*. Journal of Comparative Physiology 144: 277-286.

BUCK, J., BUCK, E., CASE, J.F. & HANSON, F.E. 1981b. Control of flashing in fireflies V. Pacemaker synchronization in *Pteroptyx* *cribellata*. Journal of Comparative Physiology 144: 287-298.

CALDER, A.A. 1998. Coleoptera: Elateroidea. In Wells, A. (ed.) Zoological Catalogue of Australia. Vol. 29.6. (CSIRO Publishing: Melbourne).

CARPENTER, J.M. 1987. Phylogenetic relationships and classification of the Vespinae (Hymenoptera: Vespidae). Systematic Entomology 12: 413-31.

1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291-296.

CHAVARRIA, G. & CARPENTER, J.M. 1994. 'Total evidence' and the evolution of highly social bees. Cladistics 10: 229-58.

DARLINGTON, P.J. 1961. Australian carabid beetles. V. Transition of wet forest faunas from New Guinea to Tasmania. Psyche 68: 1-24.

DEJEAN, P.F.M.A. 1837. Catalogue des Coléoptères de la collection de M. Le Comte Dejean 4th edition: 1-176. Mequignon-Marvis, Paris.

DE KEYZER, R. 1989. The cold light of the firefly. Australian Natural History 23(1): 50-57.

DOMAGALA, P. & GHIRADELLA, H. 1984. Structure and function of the terminal abdominal appendages (pygopodia) of photurid firefly larvae. Biologists Bulletin 166: 299-309.

ESCHSCHOLTZ, J.F. 1823. Entomographien. Naturwissenschaftliche Abhandlungen: 113-115.

EBERHARD, W.G. 1985. Sexual Selection and Animal Genitalia. (Harvard University Press: Harvard).

FABRICIUS, J.C. 1775. *Lampyris* spp. Pp. 200-202. In Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. Flensburgi et Lipsiae (Flensburg and Leipsig).

1781. *Lampyris* spp. Pp. 251-254. In Species insectorum exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adiectis observationibus, descriptionibus. 1. 552pp. Hamburgi et Kilonii (Hamburg & Kiel).

1787. *Lampyris* spp. Pp. 161-162. In Mantissa insectorum sistens eorum species nuper detectas adiectis characteribus genericis, differentiis specificis, emendationibus, observationibus. 1. 348 pp. Hafniae (Copenhagen).

1792. *Lampyris* spp. Pp. 98-103. In Entomologiciae systematicae emendatae et auctae secundum classes, ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus. 1. 330 pp. Hafniae (Copenhagen).

1801. *Lampyris* spp. Pp. 99-107. In Systema eleutheratorum secundum ordines, genera, species adiectis synonymis, locis observationibus, descriptionibus. 2, 687pp. Kiliae.

FARRIS, J.S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374-385.

1983. The logical basis of phylogenetic analysis. In Advances in cladistics. Proceedings of the Willi Hennig Society, Vol. 2' (University of Columbia Press: New York).

1988. Hennig86 Version 1.5. (Port Jefferson: New York.).

1989. The retention index and the rescaled consistency index. Cladistics 5: 417-419.

FROGGATT, W.W. 1909. Australian Insects. (Wm. Brooks & Co. Ltd: Sydney).

GAUTHIER, J., KLUGE, A. & ROWE, T. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4: 105-209.

GEMMINGER, M. & VON HAROLD, E. 1870. Luciolinae. Pp. 1650-1652. In Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Tome VI. (Williams and Norgate: London).

GERMAR, E.F. 1848. Beiträge zur Insektenfauna von Adelaide. Linnaea Entomologica III: 153-247.

GOLOBOFF, P. 1991. Homoplasy and the choice among cladograms. Cladistics 7: 215-232.

GORHAM, H.S. 1880. Materials for a revision of the Lampyridae. Transactions of the Royal Entomological Society of London 1880: 1-36, 83-112.

GUÉRIN-MÉNEVILLE, F.E. 1838. Insectes. Pp. 57-302. In Lesson, M. (ed.) Voyage autour du monde, éxecuté par ordre du roi, sur la corvette de sa majesté, La Coquille, pendant les années 1822, 1823, 1824, et 1825 etc. Zool. 2, Pt. 2, Div. 1, Ch. xiii. (Bertrand: Paris).

HANEDA, Y. 1966. Synchronous flashing of fireflies in New Guinea. Science Report of the Yokosuka City Museum 12: 4-10.

HANSON, F.E. 1978. Comparative studies of firefly pacemakers. Federation Proceedings 37: 2158-2164.

HANSON, F.E., CASE, J.F., BUCK, E. & BUCK, J. 1971. Synchrony and flash entrainment in a New Guinea firefly. Science 174: 161-164.

HENNIG, W. 1966. Phylogenetic Systematics. (University of Illinios Press: Urbana).

KALLERSJÖ, M., FARRIS, J.S., KLUGE, A.G. & BULT, C. 1992. Skewness and permutation. Cladistics 8: 275-287.

KAUFMANN, T. 1965. Ecological and biological studies on the West African firefly *Luciola discicollis* (Coleoptera Lampyridae). Annals of the Entomological Society of America 58(4): 414-426.

KIRBY, W. & SPENCE, W. 1828. An introduction to Entomology: or elements of the natural history of insects. Vol. 2, 5th edn. (Longmans: London).

KLUGE, A. & FARRIS, J. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology 18: 1-32.

LACORDAIRE, T. 1857. Histoire naturelle des insectes. Genera des Coléoptères. Tome Quatrième. (Librairie Encyclopédique de Roret. 4: Paris).

LARSON, A. & DIMMICK, W.W. 1993. Phylogenetic relationships of the salamander families: An analysis of congruence among morphological and molecular characters. Herpetological Monographs 7: 77-93.

LAPORTE, F. L. de 1833. Essai d'une révision du genre *Lampyre*. Annales de la Société Entomologique de France 2: 122-153.

LAWRENCE, J.F. & BRITTON, E.B. 1991. Coleoptera. Pp. 543-683. In Insects of Australia 2nd edn (CSIRO Melbourne University Press: Melbourne).

LEA, A.M. 1909. Revision of the Australian and Tasmanian Malacodermidae. Transactions of the Entomological Society of London 1909: 45-251.

1915. Descriptions of new species of Australian Coleoptera. Part XI. Proceedings of the Linnaean Society of New South Wales 40: 490-521.

1921a. On Coleoptera, mostly from Queensland. Memoirs of the Queensland Museum 7: 182-240.

1921b. On Australian Coleoptera of the Family Malacodermidae. Transactions of the Royal society of South Australia 45: 50-135.

1921c. Results of Dr E. Mjöberg's Swedish Scientific Expedition to Australia 1910-1913. 26. Cryptophagidae to Oedemeridae. Arkiv för Zoologi Band 14 (no. 11): 7.

1929. On Coleoptera, mostly from Queensland (Part 11). Memoirs of the Queensland Museum IX: 335-363.

LLOYD, J.E. 1966. Studies on the flash communication system in *Photinus* Fireflies. Miscellaneous publications, Museum of Zoology, University of Michigan 130: 1-95.

1971. Bioluminescent communication in insects. Annual Review of Entomology 16: 97-122.

1972. Mating behavior of a New Guinea *Luciola* firefly: A new communicative protocol (Coleoptera: Lampyridae). Coleopterists' Bulletin 26(4): 155-163.

1973a. A firefly inhabitant of coastal reefs in New Guinea (Coleoptera: Lampyridae). Biotropica 5(3): 168-174.

1973b. Fireflies of Melanesia: bioluminescence, mating behavior, and synchronous flashing. Environmental Entomology 2 (6): 991-1008.

1973c. Model for the mating protocol of synchronously flashing fireflies. Nature 245 (5423): 268-270.

1977. Bioluminescence and communication. Pp. 164-183. In Sebeok, T.A. (ed.) How Animals Communicate. (Indiana University Press: Bloomington).

1979a. Sexual selection in luminescent beetles. Pp. 293-342. In Blum, M. & N. (eds) Sexual selection and reproductive competition in insects. (Academic Press: New York).

1979b. Firefly Communication. Anima: 25-34. (In Japanese)

LLOYD, J.E., WING, S.R. & HONGTRAKUL, T. 1989. Ecology, flashes and behavior of congregating Thai fireflies. Biotropica 21(4): 373-376.

LUCAS, R. 1920. Catalogus alphabeticus generum et subgenerum Coleopterorum orbis terrarum totius, Pars 1. Archiv fur Naturgeschichte 84: 557.

MACLEAY, W. 1872. Notes on a collection of insects from Gayndah. Transactions of the Entomological Society of New South Wales 2: 239-318.

MARTIN, J.F. 1916. The thoracic and cervical sclerites of insects. Annals of the Entomological Society of America 9: 35-83.

MASTERS, G. 1886. Catalogue of the described Coleoptera of Australia. Part IV. Proceedings of the Linnaean Society of New South Wales (2)I: 259-380.

1888. Catalogue of the known Coleoptera of New Guinea, including the islands of New Ireland, New Britain, Duke of York, Aru, Mysol, Waigiou, Salwatty, Key and Jobie. Proceedings of the Linnaean Society of New South Wales (2)III: 271-334.

McDERMOTT, F.A. 1910. A note on the light emission of some American Lampyridae. Canadian Entomologist 42: 357-363.

1962. Illustrations of the aedeagi of the Lampyridae (Coleoptera). The Coleopterists' Bulletin: 21-27.

1964. The taxonomy of the Lampyridae. Transactions of the American Entomological Society 90: 1-72.

1966. Lampyridae. Pp. 98-118. In Steel, W.O. (ed.) Coleopterorum catalogus supplementa. 2nd edn. (W. Junk: Gravenhage).

McDERMOTT, F.A. & BUCK, J.B. 1959. The Lampyrid fireflies of Jamaica. Transactions of the American Entomological Society LXXXV: 1-111.

MESSENGER, S.L. & McGUIRE, J.A. 1998. Morphology, molecules, and the phylogeny of cetaceans. Systematic Biology 47: 90-124.

MONTEITH, G.B.1985. Altitudinal transect studies at Cape Tribulation, North Queensland I. Introduction and summary. Queensland Naturalist 26: 40-48.

1995. Distribution and altitudinal zonation of low vagility insects of the Queensland Wet Tropics. Part 4. Report to the Wet Tropics Management Authority. (Queensland Museum).

1997. Revision of the Australian flat bugs of the subfamily Mezirinae (Insecta: Hemiptera: Aradidae). Memoirs of the Queensland Museum 41 (1): 1-169.

MOORE, B.P. 1989. A guide to the beetles of South-Eastern Australia. Fascicle No. 9: 133-148, in Australian Entomological Magazine 16.

MOTSCHULSKY, V. de 1853. Lampyrides. Etudes Entomologiques I: 26-58.

1854. Lampyrides. Etudes Entomologiques III: 47-62.

NIXON, K.C. 1992. Clados Version 1.2. (L.H. Bailey Hortorium, Cornell University: Ithaca).

NIXON, K.C. & CARPENTER, J.M. 1996. On simultaneous analysis. Cladistics 12: 221-41.

NOVACEK, M.J. 1992. Fossils, topologies, missing data, and the higher level phylogeny of Eutherian mammals. Systematic Biology 41: 58-73.

OLIVIER, E. 1883. Lampyrides nouveaux ou peu connus. Revue D'Entomologie 3: 73-80, 326-332.

1885. Catalogue des Lampyrides faisant partie des collections du Musée Civique de Gênes. Annali del Museo Civico di Storia Naturale di Genova (2a)2: 333-374.

1886. In Baer, G.-A., Catalogue des Coléoptères des Iles Philippines. Annales de la Société Entomologique de France 1886: 183-187.

1888. Etudes sur les Lampyrides IV. Déscriptions d'espèces nouvelles. Annales de la Société Entomologique de France 1888: 47-62.

1892. Viaggio di Lamberto Loria nella Papuasia orientale V. Déscriptions de deux nouvelles espèces du genre *Luciola*. Annali del Museo Civico di Storia Naturale di Genova (2a)X: 1010-1011.

1896. Déscriptions de nouvelles espèces de Lampyrides du Musée de Tring. Novitates Zoologicae III (1): 1-3.

1902. Catalogue des espèces de '*Luciola*' et genres voisins décrits jusqu'à ce jour. Revue Scientfique du Bourbonnais et du centre de la France 15: 69-88.

1907. Coleoptera Fam. Lampyridae. Pp. 1-74. In Wytsman, P. (ed.) Genera Insectorum Bruxelles: P. Wytsman Fasc 53 74 pp.

1909a. Déscriptions de Lampyrides nouveaux du Musée Civique de Gênes. Annali del Museo Civico di Storia Naturale di Genova (3a)IV: 316-319.

1909b. Sur les *Luciola* d'Australie. Transactions of the Entomological Society of London 1909: lxxxi-lxxxii.

1910. Lampyridae. Pp. 1-68. In Schenkling, S. (ed.) Coleopterorum catalogus auspiciis et auxilio. (W. Junk: Berlin).

1911a. Le genre *Atyphella* Oll. et déscriptions d'espèces nouvelles (Col. Lampyridae). Bulletin de la Société Entomologique de France 8: 171-175.

1911b. Révision des Lampyrides. Revue Scientifique du Bourbonnais et du centre de la France 24: 24-27, 39-58, 63-85, 98-112.

1913. Lampyridae. Résultats de L'Expédition Scientifique Néerlandaise à la Nouvelle-Guinée en 1907 et 1909 sous les auspices de Dr H. R. Lorentz. Zoologie Livraison III. Nova Guinea 9: 417-422.

OLIVIER, E. & PIC, M. 1909. Lampyride et Alleculide Nouveaux. L'Echange 1909: 139-140.

OLIVIER, G.A. 1790. Entomologie, ou Histoire naturelle des Insectes. Coléoptères. Tome ii. (Baudouin: Paris).

OLLIFF, A.S. 1890. New species of Lampyridae, including a notice of the Mt. Wilson Firefly. Proceedings of the Linnaean Society of New South Wales (2)4: 643-653, 1297.

PIC, M. 1932. Résultats scientifique du voyage aux Indies orientales néerlandaises de Le prince et la princesse Léopold de Belgique. Coleoptera. Malacodermata, Byrrhidae, Heteromera (ex parte). Memoirs musee Royale du Histoire naturelle de Belgique 4(4): 85-89.

1938. Beitrag zur Kenntnis der indo-malayischen Malacodermata. pp. 3-6 in Wittmer, W. Prof. Dr. E. Handschin, Studienreise auf den Sundainsein und in Nord Australien 1930-32. Entomologische Berichten 10: 2-7.

POWELL, L.A. 1964. The Lampyridae of Australia. Unpubl. MSc Thesis, University of Queensland, St Lucia.

RADFORD, W. 1981. The Fabrician types of the Australian and New Zealand Coleoptera in the Banks Collection at the British Museum (Natural History). Records of the South Australian Museum 18: 155-197.

SIVINSKI, J. 1981. The nature and possible functions of luminescence in Coleoptera larvae. Coleopterists' Bulletin 35(2): 167-179.

SKEVINGTON, J.H. & YEATES, D.K. 2000. Phylogeny of the Syrphoidea (Diptera) inferred from mtDNA sequences and morphology. Molecular Phylogenetics and Evolution. 16(2): 212-224.

SORENSON M.D. 1996. TreeRot. (Museum of Zoology: University of Michigan: Ann Arbor).

STICKNEY, F.S. 1923. The head capsule of Coleoptera. Illinois Biological Monographs 8.

SWOFFORD, D.L. 1993. PAUP: Phylogenetic Analysis Using Parsimony Version 3.1. (Illinios Natural History Survey and Smithsonian Institution: Champaign and Washington).

1998. PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods) Version 4. (Sinauer Associates: Sunderland, Massachusetts)

TILLYARD, R.J. 1926. The insects of Australia and New Zealand. (Angus & Robertson: Sydney).

WILKINSON, M. 1995. Coping with abundant missing entries in phylogenetic inference using parsimony. Systematic Biology 44: 501-14.

1997. Character, congruence, and quality: A study of neuroanatomical and traditional data in caecilian phylogeny. Biological Reviews 72: 423-70.

WING, S.R., LLOYD, J.E. & HONGTRAKUL, T. 1983. Male competition in *Pteroptyx* fireflies: Wing-cover clamps, female anatomy, and mating plugs. Florida Entomologist. 66(1): 86-91.

WITTMER, W. 1939. Fauna Buruana. Coleoptera 7. Beitrag zur Kenntnis der indo-malayischen Malacodermata. Treubia 1(7): 21-24.

YEATES, D.K. & LAMBKIN, C.L. 1998. Cryptic species diversity and character congruence: Review of the tribe Anthracini (Diptera: Bombyliidae) in Australia. Invertebrate Taxonomy 12: 977-1078.